FACTORS AFFECTING BREEDING SUCCESS OF THE HERRING GULL (*Larus argentatus* PONT.) AT AN INCREASING AND A DECREASING COLONY.

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Presented in candidature for the degree of Doctor of Philosophy to the Faculty of Science, University of Glasgow, August 1992.

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CANDIDATES DECLARATION

I declare that the work recorded in this thesis is entirely my own unless otherwise stated and that it is of my own composition. No part of this work has been submitted for any other degree.

29/9/92

DEDICATION

To Lou

ACKNOWLEDGEMENTS

First of all I would like to thank my supervisor Pat Monaghan for five years of fearless criticism !

For help with my fieldwork, I would like to express my deep appreciation for the help and friendship of the people at Sanda and at Walney. Life on Sanda was made possible by the support of the larger (lager ?) than life Cameron MacLean and the lighthouse keepers, particularly Jimmy Shanks - provider of coal, Rizlas and endless banter. Gordon Liddle deserves special thanks for hard work, practical ideas and being able to cope with life with a manic Armstrong. He also provided one of the most amusing hang-overs I have ever seen ("must have been something in the water"). The smug fop Sean "would'nt it be better if you did it this way" Twiss, deserves reluctant thanks for always being right and pointing out the bleeding obvious (alright, gulls don't eat grass or defy gravity). He also managed to rationalise my fieldwork and was particularly good when it came to handling hazardous substances. A very big thanks to Lucy Gilbert for her hard work on Sanda and her ability to "mellow me out" when things got a bit frantic (although I don't think you should have rejected my pom skua record).

Walney folk were lovely and made my stay there most enjoyable, so thanks to Ziggy, Tim, Tish and Bryan. Particular thanks have to go to Esther "Duck-pond" Scott and again, Lucy Gilbert, for helping out when I wasn't very well. Sean also helped again.

My deepest thanks have to go out to the Tennents "Bird Bath" members; my partner in gastric pain Rob Field, Chris "Elmore James" Thomas, Graeme "What is for supper" Austin, Alan "Dr Feelgood" Reichelt, Gwenda "Weight-on" Hughes, Jayne "Everybody Dance" Tierney, Clive "I've come back to write-up" McKay, Roddy "Do you wanty to see my little snake" MacDonald, Alan "aceeeeed" Scott, *et al.*

Thanks also go to Arthur Cain, Geoff Parker, Eric, Lemmy and Frank for making me do it. Thanks to my Mum and Dad for having me. For the final inspiration that enabled me to tackle the nightmare of writing-up, the biggest thanks of all go to Claire McCaul.

CONTENTS

SUMMARY

(1) The breeding success of Herring gulls was studied at a decreasing (Walney Island, Cumbria, in 1989) and an increasing colony (Sanda Island, Argyll, in 1990) to establish whether differences in breeding performance could account for the differences in population dynamics. No differences were found in laying date, hatching success, chick growth rates or fledging success per brood. Differences were found however in the volume of the *a* and *b* eggs from clutches of three (larger at Walney), the survival of *c* chicks (lower at Sanda), although these did not lead to a difference in overall breeding success between the colonies. The differences in population changes at each colony do not appear to be the result of differences in breeding success.

(2) At both colonies, clutch size, egg volumes, hatching success, chick survival and fledging success per brood were very high by comparison with earlier studies in Britain. Egg volumes at Walney were the highest yet reported from a colony where no culling has taken place, suggesting that availability of food immediately prior to egg-laying, is very high.

(3) The proportion of birds breeding in third year plumage was recorded at both colonies. None were found at Sanda, however the proportion breeding at Walney was the highest recorded at a colony where culling had not taken place. The proportion was similar to that found in colonies where extensive culling had taken place e.g. Isle of May, suggesting that competition for nesting territories and food was low at Walney in 1990.

(4) Examination of the diet of incubating adults revealed large differences in the diet at the two colonies. At Sanda, most of the food came from farmland (earthworms and barley), whereas at Walney the main component of the diet was refuse. The main component of chick diet at both colonies was fish. At Sanda these were gathered from behind Norway Lobster boats, while at Walney, they appear to come from Fleetwood fish

docks. The second largest component of chick diet at Sanda was sandeels, and at Walney, refuse. Sandeels were caught either directly by the adults around Sanda, or stolen from auks, particularly Razorbills.

(5) Changes in chick diet with chick age were studied. Earthworms formed a large part of the diet of small chicks (< 1 week post-hatch at Walney, < 2 weeks post-hatch at Sanda). As chicks grew the composition of their diet changed, with the proportion of sandeels in the diet increasing with age at Sanda, and the proportion of refuse in the diet increasing at Walney. The amount of fish in the diet did not change with chick age at either colony. These changes in diet were found to be independent of seasonal changes in food availability.

(6) The availability of the three main components of the diet at Sanda have all increased during the period of population growth. In particular, the Norway Lobster fishery has increased rapidly coincidental to the period of most rapid population expansion, suggesting that the population growth is a result of increased food availability. The availability of refuse at Walney has decreased during the most recent decreases in the gull population, as a result of both a decrease in the absolute volume tipped and more rapid burial of refuse in recent years.

(7) The cause of decline at Walney appears high levels of mortality due to infection by *Clostridium botulinum*, causing botulism. This explains the observed similarities between this study and studies at colonies where extensive culling has been carried out, particularly in the large egg volumes and number of third year birds found breeding. It also explains why the Lesser black-backed gull has declined less rapidly than Herring gulls at Walney as they feed less on refuse. Sanda gulls in spite of sharing common wintering areas with Walney Herring gulls, have not declined as botulism occurs most often in the summer or before dispersal to winter quarters.

(8) Differences in breeding parameters between eight sample plots were studied at Sanda to assess the reliability of using sample plots to measure population breeding success. Large differences were found between study plots for median laying date (range = 9 days), mean total clutch volume of 3-egg clutches (9%), mean hatching success per 3-egg clutch (1.4 chicks) and mean fledging success per brood of three chicks (0.88). To establish whether the observed differences in breeding success could be the result of differences in nesting habitat between colonies, the effect of nesting habitat on breeding success was investigated. Three aspects of habitat quality were recorded for each nest in each colony, the amount of cover around the nest available to shelter incubating/brooding adults or unattended eggs, the availability of cover for small chicks (< 1 week post-hatch), the availability of cover for large chicks (up to fledging). The availabilities of each of these varied between sample plots; however none of these had any effect on breeding success.

(9) The relationship between nest density and breeding success was recorded at three sample plots. Nest density had no effect on breeding success, probably as a result of very low density recorded at Sanda.

(10) Using a combination of Total Clutch Volume (T.C.V.) and laying date, the relative ages of birds breeding in the eight sample plots on Sanda was estimated. The pattern of spread of nesting gulls on Sanda that this technique predicted, closely matched the known pattern of spread, suggesting that this technique is reliable.

(11) The effects on breeding success of laying date, clutch size, individual egg volumes and T.C.V., were investigated (the last three at Sanda only). Laying date had no effect on clutch size, hatching success and fledging success at Sanda, and no effect on clutch size at Walney. The volume of *c* eggs and T.C.V., both declined as the season progressed at Walney, but not at Sanda. Birds laying 2-egg clutches had lower hatching success, chick survival and overall fledging success than birds laying 3-egg clutches. Individual egg volumes and T.C.V. had no effect on hatching success or chick survival. The lack of

observed relationships between breeding parameters such as laying date and clutch size appeared to be due to the high breeding success at both Sanda and Walney. Examination of results from other studies suggest that these relationships are not found in years of high breeding success. In view of this, the way that Herring gulls can increase their reproductive output by altering energy investment at the egg-laying stage are examined. The conclusion is reached that Herring gulls are constrained in the way that they organise their reproductive output, in contradiction to conventional theories of avian reproductive biology.

(12) Using the observed pattern of reproductive organisation from this study, and the results of other studies, the current theories regarding hatching asynchrony and clutch size in gulls is examined. None are consistent with what is known of Herring gull breeding biology. An alternative hypothesis is offered. This hypothesis predicts that the prey fed to chicks during the first week post-hatch does not offer the same return in terms of energy or nutrients, per unit adult foraging time, as food fed to older chicks. As a result, Herring gulls organise their reproductive effort so as to maximise hatching synchrony so that the period during which at least one chick is less than one week old is reduced. This hypothesis is consistent with the known pattern of reproductive organisation in Herring gulls. This "Expensive Babyfood Hypothesis" makes several exclusive predictions that were tested experimentally at Walney.

(13) Synchronous-hatching was induced in a sample of broods by taking three eggs from different nests that were close to hatching, and forming composite clutches. The resultant broods fledged more chicks per brood than did un-manipulated control broods. This increased fledging success was due to the improved survival of the *a* and *b* chicks, and is consistent with the E.B.H. but no other hypothesis.

(14) A sample of broods of three at Walney were fed Kit-e-Kat during the first week post-hatch. These broods fledged more young than did control broods of three chicks. Adult

attendance during the first week post-hatch was higher at supplementary fed nests, with a higher proportion of records of two adults attending simultaneously, and fewer records of absence of both adults. The difference disappeared in the second week post-hatch, after the supplementary feeding had stopped. This result is consistent with the E.B.H. and no other hypothesis.

(15) The relationship between adult attendance at the nest and brood age was studied by observing a number of nests through to fledging. This showed that absence of both adults occurred more often with broods less than 1 week post-hatch, and that attendance of both adults simultaneously occurred less often. These results suggest that adults spend more time foraging during the first week post-hatch and therefore support the E.B.H.

(16) A key prediction of E.B.H. is that gulls cannot achieve full hatching synchrony by delaying incubation until the last egg is laid. This was tested by removing the first laid egg to prevent incubation. The egg was then replaced when the second egg had normally been laid. Eggs were stored at ambient temperature to simulate nest conditions. Eggs that were not incubated showed a very low hatching success by comparison with other eggs in the same clutch, and published figures. This suggests that gulls are not able to achieve full hatching synchrony through delayed incubation.

(17) All of the predictions made by the E.B.H. were supported by the experimental results. None of these results are consistent with conventional theories suggesting that the E.B.H. currently offers the best explanation for the pattern of reproductive organisation observed in Herring gulls and other larids.

CHAPTER 1

INTRODUCTION

Introduction

The Herring Gull in Britain has undergone two major changes in its population size and distribution this century. During the early part of this century its numbers increased while its range extended around the British coastline, until by the time of the first national survey in 1969/70, over 335,000 pairs were found nesting in nearly all coastal counties (Cramp *et al.* 1974). At the same time, populations in other Northern European countries were also undergoing dramatic increases e.g. In Holland (Voous 1960, Spaans 1971) and Germany (Goethe 1964).

The cause of these increases was not clear, several authors linking the population expansion to increased food availability, (Parslow 1967, Harris 1970, Monaghan 1976, Mudge 1976) as a result in increased fishing activity and changes in fishing activities (Harris 1970), tipping of domestic refuse (Monaghan 1976) and dumping of sewage at sea (Monaghan and Zonfrillo 1986). The timing of the increase did not coincide with any particular increase in the availabilities of these food types, leading some authors to suggest a time lag in the Herring gull's ability to learn to exploit these new opportunities (Harris 1970, Mudge 1976). A decrease in Human persecution was also thought to have facilitated population growth as a result of decreased egg-collecting (Harris 1970), shooting for "sport" (Mudge 1976) and killing for feathers for the millinery trade (Mudge 1976).

By the second British survey in 1985-1987, the numbers had dramatically reduced to an estimated 181,000 pairs, an overall decline of 46%. This decrease was not evenly spread through the Herring Gull's range; some areas suffered huge declines e.g. the Welsh population declined from 48,600 pairs to 10,700 pairs, a fall in numbers of 78% (Lloyd *et al.* 1991), while in other areas the population increased over the period e.g. in Argyll and Bute, the population increased from 11,004 pairs to 17,202 pairs (Lloyd *et al.* 1991). The reasons for this recent decrease and the pattern of changes through the British Isles have not been established, although Lloyd *et al.* (1991), suggested that the increased

occurrence of botulism may have produced large scale mortality.

Furness *et al.* (1988) suggested that the increase in the Clyde Sea area could be due to increased fishing activity for Norway Lobster (*Nephrops norvegicus*). He showed that the mean size of fish discarded from trawlers fishing for Norway Lobsters was smaller than that for Whitefish and Herring boats. This smaller size allowed Herring gulls to achieve improved "scavenging" success as they were able to swallow discards quickly and thus avoid klepto-parasitism, and more able to compete with larger species such as Gannets (*Sula bassana*) and Great Black-backed gulls (*Larus marinus*).

To investigate the causes of population changes in the Herring gull, I studied diet and breeding success in two colonies, one a declining colony and the other an increasing colony. The increasing colony I chose was Sanda Island, Kintyre, where I worked in 1989. This is one of the largest colonies on the West coast of Scotland and also one of the most rapidly growing (Lloyd *et al* 1991). The study of a decreasing colony was made at Walney Island, Cumbria, in 1990. This was formerly the largest breeding colony in Britain (Cramp *et al.* 1974), but has recently undergone a dramatic decrease (Dean 1991, Lloyd *et al.* 1991).

Population changes - Sanda and neighbouring islands

Unless otherwise stated details are taken from Gibson (1983). Herring gulls breed on all of the three islands of the Sanda group. As the population changes on these islands have differed between the islands (Figure 1.1), I will discuss these individually.

Glunimore

Of the Sanda group of islands, breeding was first recorded from Glunimore in 1898 when "nearly 50 pairs" were found. Since then the numbers have remained relatively stable with 40 pairs in 1951 (Borland and Walls 1951), 50 pairs in 1955, 1964, and 1969. Maguire

Figure 1.1 The numbers of pairs of Herring gull nesting on each of the 3 islands of the Sanda Group, Kintyre, since colonisation.

(1981) estimated the population to be 100 pairs in 1980. Systematic nest counts on Glunimore were not attempted in 1989 due to the disturbance this would cause to nesting Cormorants (*Phalacrocorax carbo*) and Guillemots (*Uria aalge*), but observations from Sanda and during brief visits to Glunimore suggested that approximately 50-60 pairs were nesting. Glunimore is an extremely small island (see study sites, Chapter 2) and it is difficult to see how more than this number of pairs could nest without extra nesting habitat having been available. Since Maguire's estimate, the numbers of Guillemots nesting on Glunimore has increased to the point where they now occupy all of the boulder beach around the island. I can only assume that this area must have been previously occupied by Herring Gulls, and that these were displaced by the increasing Guillemots.

Sheep Island

Breeding was first recorded in 1900, when 20 pairs were found. A period of steady increase then followed, with "at least 100 pairs" in the early 1940's, "at least 200 pairs" in 1951 (Borland and Walls 1951), and 400 pairs in 1955 and 1956. After 1956 large numbers of eggs were collected in an attempt to control the population and numbers declined, with 150 pairs in 1964 and a slight recovery in 1969 with 200 pairs. Control measures were then abandoned and since then egg collecting has only been carried out by a small number of local fishermen. The population has increased during the subsequent period to 1000 pairs in 1980 (Maguire 1981). I visited Sheep island briefly during 1989 and from a rough count of sitting birds in the main nesting areas, estimated the population to be in the region of 1000 pairs, with nesting birds occupying all available nesting habitat. Conversation with Eddie Maguire confirmed that this was also the case in 1980. Whilst this might suggest that the population on Sheep Island has not changed much, colony growth in gulls often results from increases in nest density rather than colony area (Becker and Erdelen 1986) so this interpretation is too simplistic. I consider my estimate to be a conservative one and while the population was not accurately censused I feel confident that it has not declined since Maguire' estimate.

Sanda

Breeding was not confirmed on Sanda until "a few pairs began to nest" in the early 1940's. A slow increase occurred thereafter with 15 nests in 1951 (Borland and Walls 1951), 20 pairs in 1955, 1958 and 1964. After this time the local farmer tried to control the population by egg-collecting and in 1969 only 2 pairs nested. In the early 1970's control measures ceased, since when numbers have dramatically increased, with 100 pairs in 1972 and 800 pairs in 1980 (Maguire 1981).

In 1989 I counted the population using a combination of two techniques. In all of the colonies away from the large colony situated on the South-east coast (see study sites, Chapter 2), nests were counted during the season by marking the nearest large rock with spray paint and recording the number of new nests marked on each visit to the colony. As these colonies were visited regularly for egg/chick measurements, this resulted in very little extra disturbance and could be used during routine monitoring. In the large South-east coast colony, only small areas were monitored in this way. Due to the large size, variation in width and wide variation in nesting density, I felt that measuring the nest density and colony area to calculate the total population, would result in an unacceptably inaccurate count. Instead, a count of apparently occupied sites (A.O.S.) at the end of May was made. Due to the large size of the colony and thus the time required to make a complete count, the count was carried out only once. Observations at smaller colonies where the positions of nest-sites were known suggested that this technique was accurate as at least one adult was always on territory during incubation and very few adults sat away from their territories.

These surveys revealed that in 1989, there were 1414 pairs of Herring gulls nesting on Sanda, made up of 1130 A.O.S.'s in the colony on the South-East coast and 284 nests in scattered bays around the rest of the island. This confirms that the dramatic increase at Sanda was still continuing in the year of study, 1989, with an annual mean increase of 7% per year since

Table 1.1 Changes in the population of breeding Herring gulls at South Walney, since colonisation.

Year	Breeding pairs	Source
1920's	1	Brown (1967)
1950's	c1000	"
1965	9250	"
1969	17500	MacRoberts and MacRoberts (1972)
1974	23500	Vermeer (1977)
1978	22000	Dean (1991)
1982	16000	"
1984	12000	"
1985	9000	Birds in Cumbria*
1986	10000	"
1987	10000	"
1988	8000	"

* Annual report published by the Association of Cumbrian Natural History Societies.

Figure 1.2a Number of pairs of Herring gulls breeding on South Walney 1900-1990.

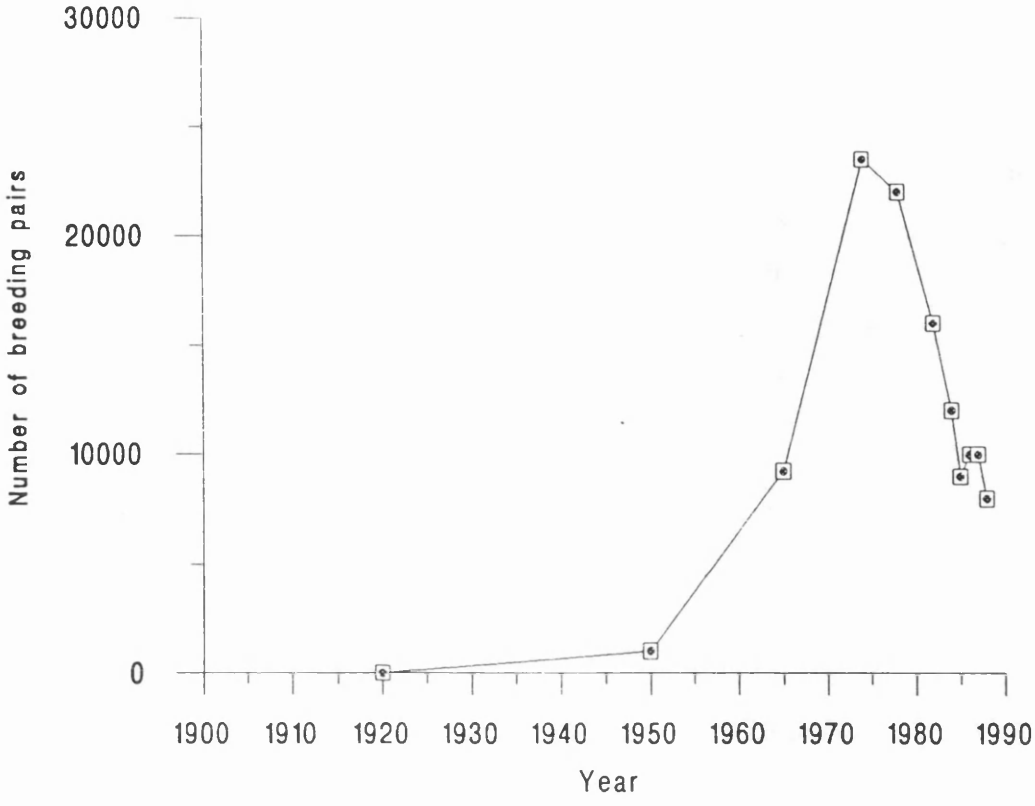
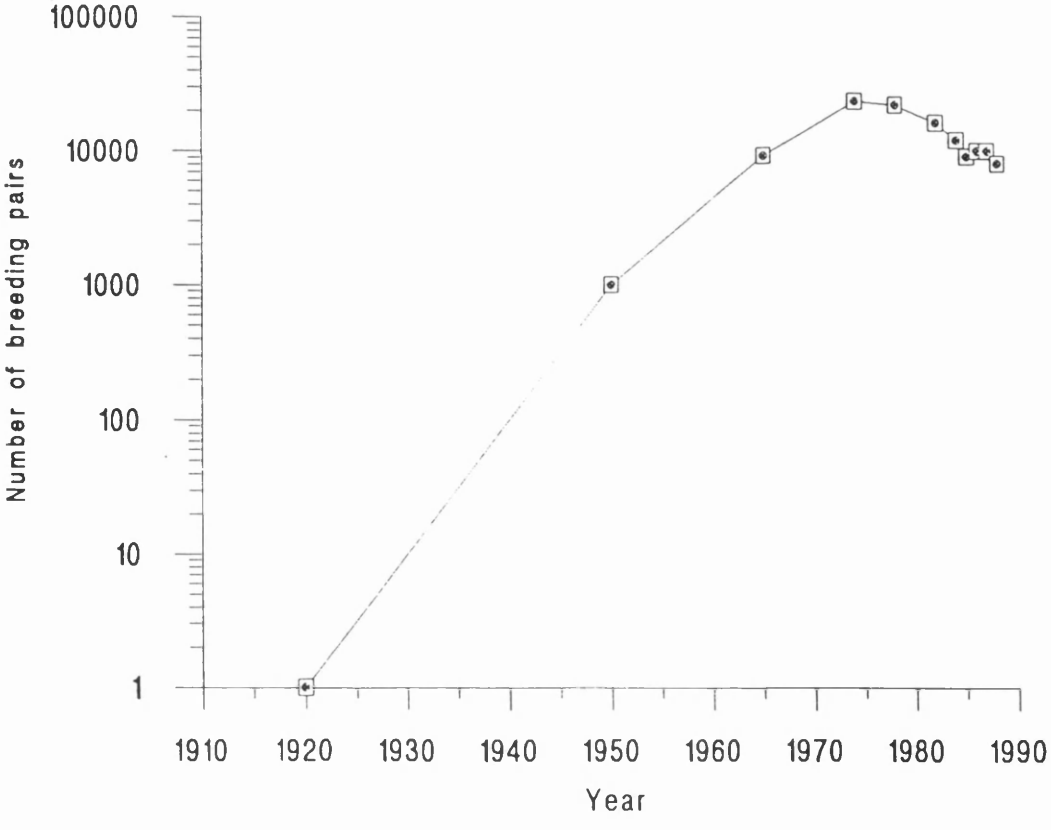


Figure 1.2b The growth of the breeding population of Herring gulls at South Walney 1900-1990.



giving a total increase of 77%.

Population changes - Walney

The dramatic growth of the population at Walney has been described in Brown (1967), Vermeer (1977) and (Dean 1991). Changes in the number of breeding pairs since colonisation, are presented in Table 1.1 and Figure 1.2. The population growth was particularly dramatic between 1950 and 1965, when the increase averaged 25% per year. Using estimates of breeding success and adult/immature survival at Walney, Brown estimated that the maximum annual rate of increase due to recruitment from the Walney breeding population would be 9.5%. As this was considerably lower than the observed growth, he concluded that the population growth at Walney must have been at least in part, due to massive immigration. After the study by Brown, the population further increased until there were 23,500 pairs in 1974. However, since then, the population has undergone a period of rapid decline, with the 1988 population being just over a third of the 1974 population, a reduction of 15,500 pairs in 14 years.

Aims

The aim of this investigation was to study factors affecting breeding success at each colony. The diet of incubating Herring gulls and of chicks was examined at both colonies, to establish whether changes in food availability could have produced the different patterns of population change at each colony. At Sanda, the way in which physical factors such as territory size and cover around the nest affect breeding success was also studied, as was the way in which birds organise their reproductive investment at the egg-laying stage. The results from the study of diet, chick survival and the way in which Herring gulls organise their reproductive effort, suggested that the availability of food for chicks less than 1 week old was the limiting factor in chick production. This was as tested experimentally at Walney, by manipulations of food availability and reproductive organisation.

CHAPTER 2

STUDY SITES AND METHODS

INTRODUCTION

STUDY SITE - SANDA

The Sanda group of islands lie approximately 1 mile South of the Kintyre peninsula in Argyll, Scotland (Figure 2.1 grid ref. NR 00,70). The group consists of 3 islands, Sanda, Glunimore and Sheep Island (Figure 2.2). Of the 3 islands only Sanda is inhabited, having a manned lighthouse on the South coast. Due to hazardous landing conditions and strong tidal "rips" and currents around the islands, it was not possible to visit Glunimore and Sheep Island often enough to use these as study sites, therefore all of the work was carried out on Sanda.

Sanda is 1.5 miles long and is covered by a combination of grazed Heather *Calluna vulgaris* and rough grassland (mostly *Nardus spp.*), providing few foraging opportunities for Herring Gulls. The coastline is mostly boulder-beach with several steep slopes and rocky outcrops. On the north coast of the island, extensive areas of rock are exposed at low tide, as are reefs covered in stands of Kelp *Laminaria* all around the island. Strong tidal upwellings occur between Sanda and Sheep Island, in the Sanda channel, East of Glunimore and South of Sanda (Figure 2.2). On several occasions these upwellings were the site of very large concentrations (>1000 birds) of feeding seabirds, including; Fulmar *Fulmarus glacialis*, Manx Shearwater *Puffinus puffinus*, Gannet *Sula bassana*, Shag *Phalacrocorax aristotelis*, Lesser Black-backed Gull *Larus fuscus*, Great Black-backed Gull *L. marinus*, Kittiwake *Rissa tridactyla*, Guillemot *Uria aalge* and Razorbill *Alca torda*. All of these species breed on the Sanda group, except the Gannet which breeds on Ailsa Craig 20 miles SSE. Other species breeding on the Sanda group include Storm Petrel *Hydrobates pelagicus*, Cormorant *Phalacrocorax carbo*, Common Gull *L. canus*, Black Guillemot *Cepphus grylle* and Puffin *Fratercula arctica*). On Sanda, Herring gulls nest amongst the boulder beaches which surround most of the island.

Figure 2.1 Sanda and the Kintyre peninsula.

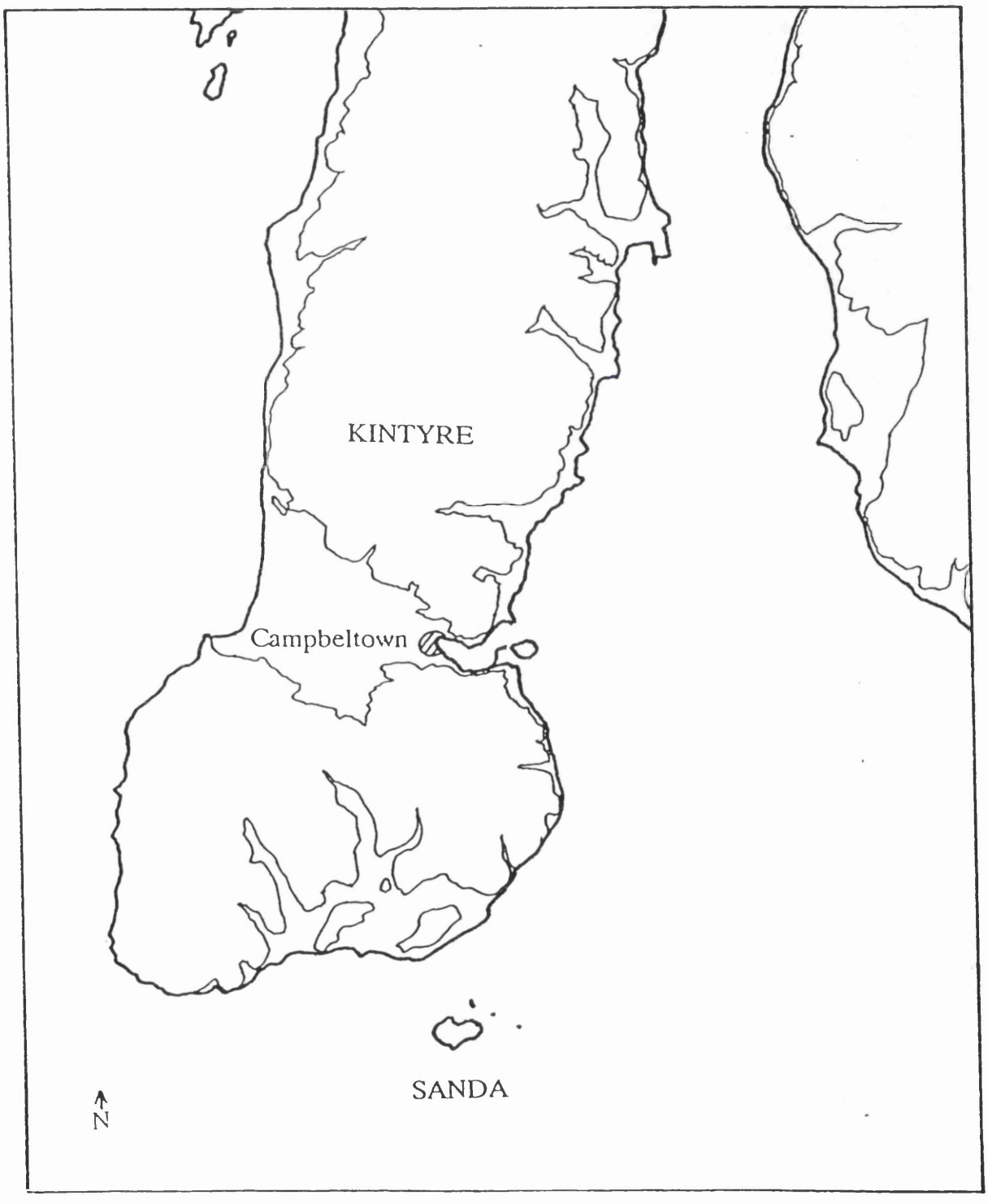
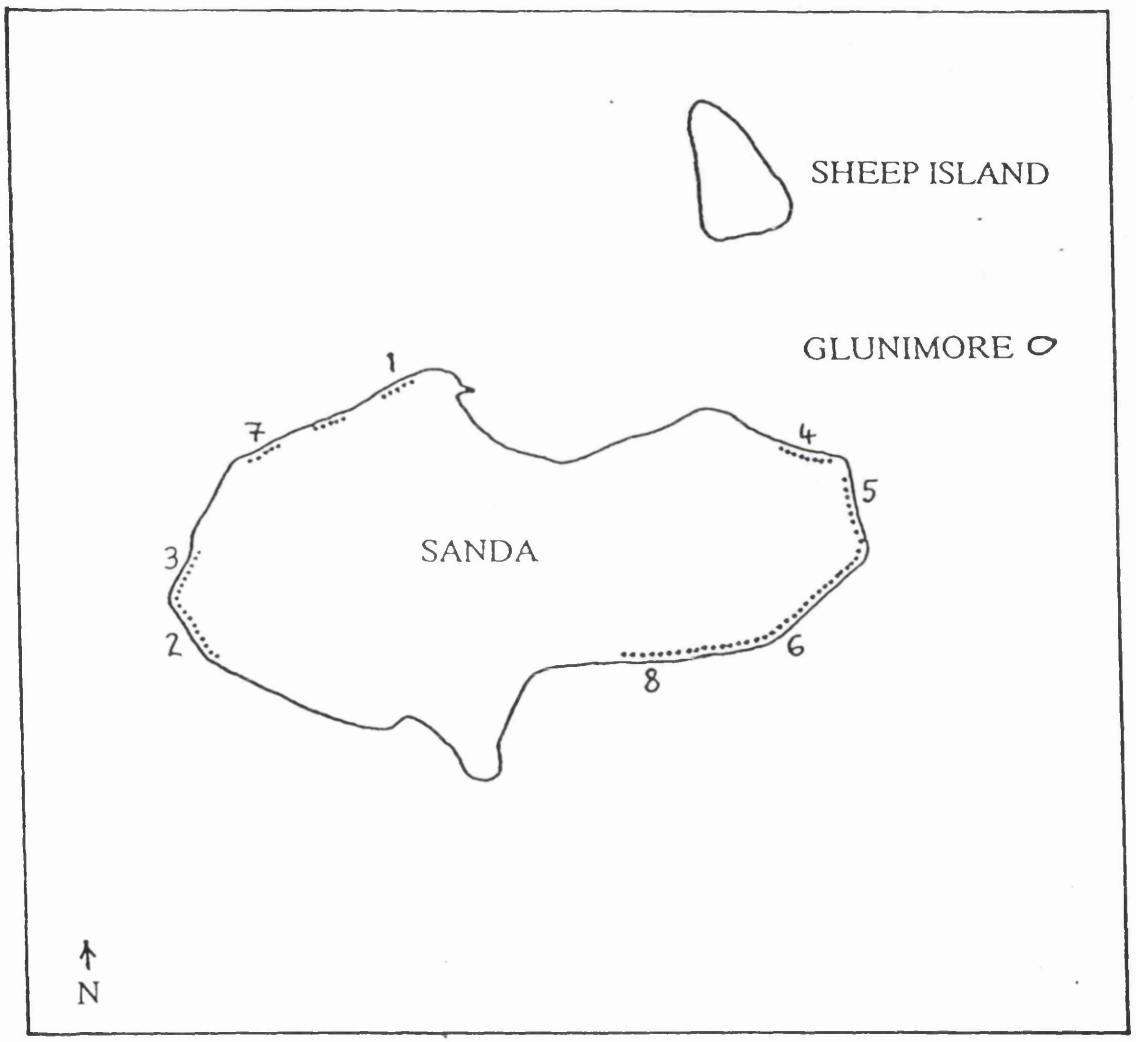


Figure 2.2 The Sanda group of islands, showing the distribution of nesting Herring gulls (dotted areas)and study plots on Sanda.



Scale: 1 inch = 0.5 miles

Herring Gulls breeding on Sanda have little opportunity to exploit human refuse, with Campbeltown being the only sizable town within reasonable flying distance i.e < 40 miles (Figure 2.1). Campbeltown is also home to a small fishing fleet, providing possible sources of discarded fish and offal. The Clyde Sea area is home to a major fishery for pelagic fish (mostly Herring *Clupea harengus* but also Mackerel *Scomber scombrus* and Sprat *Sprattus sprattus* Bailey *et al.* 1986), demersal fish (mostly Cod *Gadhus morhua*, Whiting *Trisopterus luscus*, Saithe *Pollachius virens*, Hake *Merluccius merluccius* and Haddock *Melanogrammus aeglefinus* Hislop 1986) and crustaceans (*Nephrops norvegicus* (Bailey *et al.* 1986) and recently *Macropipus puber* and *Cancer pagurus*). Of these types of fishery, the pelagic fishery has declined dramatically since a peak in the Clyde in the 1970's (R.S. Bailey *et al.* 1986). The far less important demersal fishery appears also to be in decline. The fishery for crustaceans however is increasing rapidly (Hislop 1986).

The Kintyre peninsula is not intensively cultivated, most of the land being over 200 feet (Figure 2.1). Agriculture in these areas is mostly either sheep-farming or forestry, neither of which provide opportunities for Herring gulls to forage. In the lower lying area of the southern tip of Kintyre and the area west of Campbeltown, most of the agriculture is either arable (almost totally Barley) or grass grown for sileage. These farming practices offer the gulls the opportunity to feed on grain and invertebrates, particularly during ploughing, sileage cutting or hay making.

STUDY SITE - WALNEY

The study at Walney Island, Cumbria (Grid Ref. SD 20 60. Figure 2.3), was carried out on the Cumbria Wildlife Trust's reserve at South Walney. This reserve is a large dune system that supports a large population of Herring Gulls (8000 pairs in 1988 (Dean 1991)) and Lesser Black-backed Gulls (17,000 pairs in 1988 (Dean 1991)), with smaller nesting populations of Great Black-backed Gulls and Terns (*Sterna* spp.). Exhaustive descriptions of the colony are provided in Dean (1991). The area around Walney offers several possible food sources to gulls, particularly the large areas of tidal mud-flats and mussel

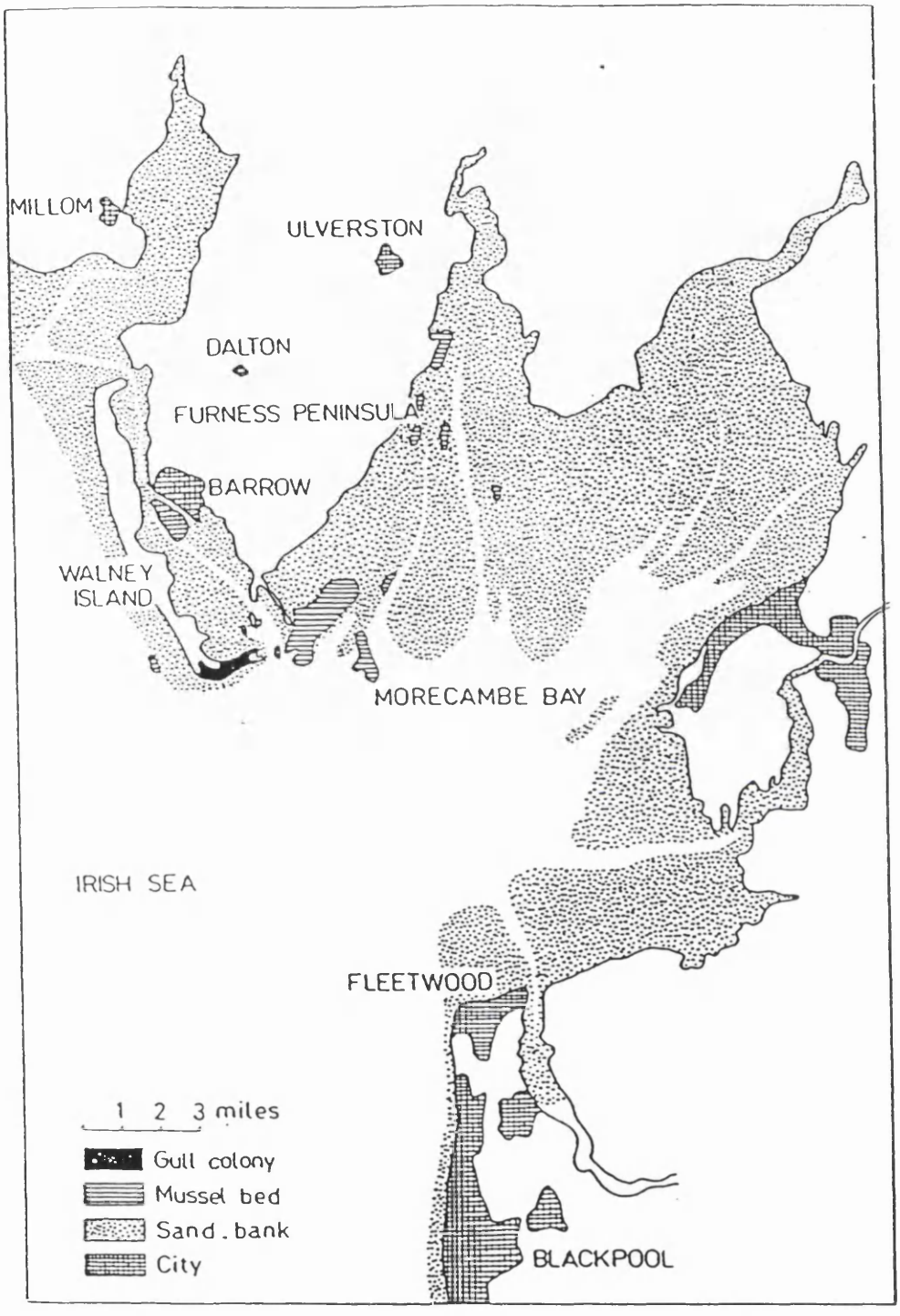


Figure 2.3 The location of the Walney gull colony in relation to local feeding areas (reproduced from Vermeer 1977).

of the colony are provided in Dean (1991). The area around Walney offers several possible food sources to gulls, particularly the large areas of tidal mud-flats and mussel beds in Morecambe Bay; the refuse tip at Walney; the fish docks at Fleetwood and the areas of pastureland on the Furness peninsula. Detailed descriptions of these foraging areas are given in Vermeer (1977) and Sibly and McCleery (1983a).

METHODS

The methods presented in this chapter are the general methods used to collect data used in analyses in more than one of the following chapters. Where methods are limited to work described in only one chapter, they will be explained in that chapter.

Study plots

Eight study plots were chosen on Sanda (Figure 2.2). These included 5 discrete sub-colonies that were isolated from each other either by physical features e.g. rocky headlands (study plots 1, 2, 3 and 7), or areas where no gulls nested (study plot 4). The remaining 3 study plots were situated within the largest single colony on the South-east coast (plots 5, 6 and 8).

On Walney my choice of study plot was constrained as I could only work in one area (c500 metres south of the warden's cottage, extending approximately 750 metres South-east, with a maximum width of c300m). South Walney nature reserve is open to the public, and this was the only continuous area of gullery where I was away from both the public's gaze and sensitive species (particularly terns) prone to disturbance while breeding.

Nest Histories

On Sanda, individual nests were marked as soon as the first egg was present in the nest. Nests were marked using individually numbered 15-20cm wooden stakes placed 1 metre from the nest, either hammered into soft substrate or jammed between rocks as conditions

required. Nests were visited at three day intervals in strict rotation to avoid introduction of biases as a result of differences in the number of visits to nests.

Laying date was taken as the first day on which an egg was recorded in the nest. Eggs were marked either A, B or C by laying order (and will be hereafter referred to as *a*, *b* and *c* respectively, as will chicks where hatching order was known), using a waterproof marker pen. Laying order was recorded for each egg where possible; however on many occasions two eggs were laid between visits. No attempt was made to classify these eggs into laying order even though it is known that eggs in a clutch normally vary in size with laying order (e.g. Parsons 1976). Analyses of eggs by laying order only include eggs where laying order was definitely ascertained, therefore sample sizes for *a*, *b* and *c* eggs differ.

Egg volumes were recorded using callipers to measure maximum length and maximum breadth to the nearest 0.1mm. Volume was then calculated using the equation

$$\text{Volume} = \text{Length (mm)} \times \text{Breadth (mm)}^2 \times 0.00476$$

The correction factor (0.00476) is taken from Harris (1964).

During the study at Sanda six 1-egg clutches were found. These were monitored routinely; however on no occasion was an adult seen to incubate any of these eggs, and on all visits the eggs were found to be cold (eggs from larger clutches were normally warm on handling even after adults had been off the nest for > 15 minutes). It was therefore assumed that these nests represented abandoned nesting attempts in agreement with Harris (1964), and they were excluded from calculations of clutch size for comparisons between colonies and sample plots.

After laying, nest visits continued at 3 day intervals, with the nest contents recorded on each visit. Hatching date was taken as being the first day on which a chick was recorded in the nest unless the chick was fully dry in which case it was assumed to have hatched the previous day. Daily observations of a group of non-study nests suggested that this was an

accurate method. Where eggs survived the incubation period and then disappeared at the predicted time of hatching, the chick was assigned to the category "presumed hatched". A discussion of this category is given in chapter 5. Due to nests only being visited at 3 day intervals, hatch order was often impossible to ascertain for the whole brood, as more than 1 chick would often hatch between visits. Where two chicks had hatched between visits, it was often possible to assess which was the older by examining the chicks to see how much the plumage had dried out post-hatch. It was often however only possible to establish the definite position in the hatching order for 1 chick. For this reason, the sample sizes for known hatch order chicks differ from each other and from the sample sizes where hatching order was not required for the analysis.

Chicks were individually marked using tags made from strips of dymo tape stapled together around the tarsus (Figure 2.4). On each tag the number of the nest and the position of the chick in the hatch order was written using waterproof marker-pen or a dymo gun (dymo guns were abandoned when it was found that they weakened the tape and that this method took longer than simply writing on the tape). The tags were not hard-wearing and chicks normally had to have tags replaced once during the four weeks of study. The positioning of the staple allowed the tag to split as the tarsus thickened, preventing the leg from being constricted. If tags were not able to slide freely up and down the tarsus, they were adjudged too tight and replaced. Tags appeared to have a minimal effect on the chicks, only on one occasion did I see a tag result in any harm to a chick, when a tag became caught in vegetation and the chick subsequently died.

When tags were removed, it was found that the area under the tag was less pigmented than the rest of the leg. No chicks were found without tags and with this lighter area on the leg. It was therefore assumed that apparent disappearance of chicks was not due to tag loss. When chicks were four weeks old, the tags were removed.

Territories were visited at 3 day intervals after hatching, and each chick found was

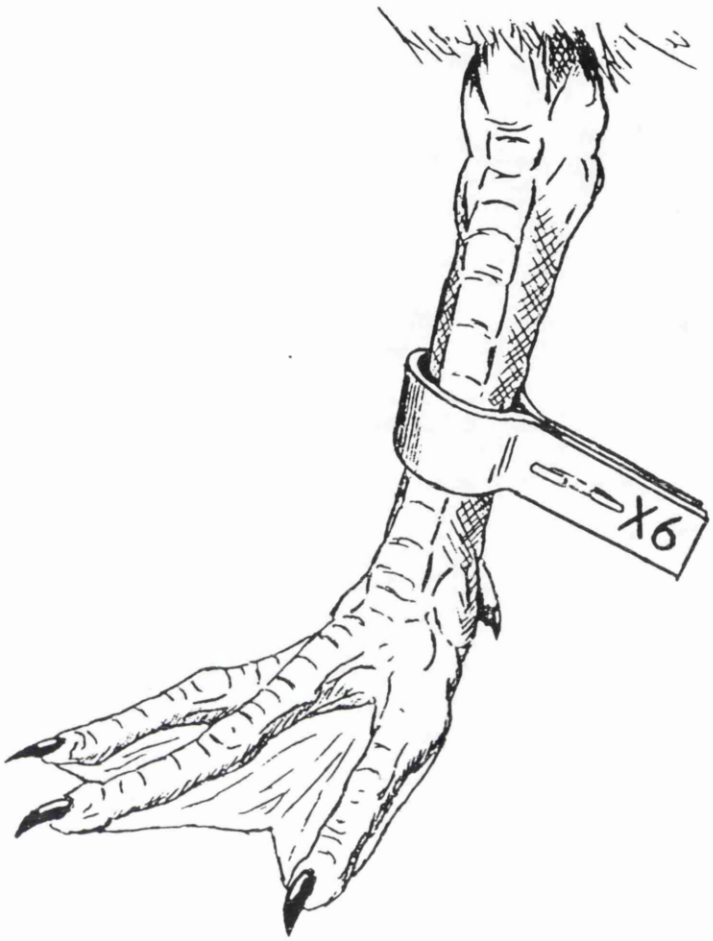


Figure 2.4 - Dymo tape leg flag used to identify chicks

weighed and measured. Prior to weighing each chick was examined to determine whether the chick had food in the crop. If this was the case, the food was massaged up the oesophagus until the chick regurgitated, so that in all cases chicks were weighed "empty". In the majority of cases this was not necessary as chicks would regurgitate as soon as they were handled. Regurgitates that could be identified in the field, were left next to the nest for adults to re-ingest. Regurgitates that could not be identified immediately were taken back to the laboratory for further examination.

Chicks were weighed using appropriate spring balances; to the nearest 1g for chicks <200g and to the nearest 5g for chicks >200g but <1500g. Total head and bill (T.H.B.) was also measured to the nearest 0.1mm using callipers (following Coulson *et al.* 1983). Chick survival, chick weight and T.H.B were recorded until the chicks were four weeks old, after which time the tags were removed and the chicks left alone. Any chick older than four weeks that was seen with a tag, was captured and the tag number recorded before removal. Chick survival and growth was only monitored until the chicks were four weeks old, because after this time they became difficult to catch as many chicks would either enter the sea (and become soaked), or run considerable distances from their territory. Chicks returning to their own territory would have to pass through neighbouring territories where they would be attacked by neighbouring adults. Both of these factors would have artificially reduced chick survival. Survival after four weeks post-hatch is generally high in Herring Gulls, so the resultant over-estimate of fledging success is likely to be very low (fledging normally occurs at 35-40 days post-hatch. Mortality during the period between four weeks post-hatch and fledging is less than 5% (Kadlec and Drury 1968, Davis 1975).

Nest histories - Walney.

Nest histories at Walney were recorded in the same way as at Sanda, except that nests were visited daily around the time of hatching so that hatching order could be accurately

ascertained. Chicks at Walney were also provided with chick shelters to minimise the effects of observer disturbance, and to allow easy capture. The shelters were made from commercial pear boxes (kindly donated by Asda's Barrow in Furness branch) sawn in half and inverted. These were held in place by a cane pushed through a drilled hole in the top and then into the soil beneath. Providing the shelters made capture of chicks easy as they would normally run into the shelter on my approach and again after release. The provision of chick shelters is unlikely to have had any effect on fledging success, as chicks had plenty of cover within the study territories. This was in the form of Rabbit holes and Nettle beds. Chicks are easier to catch in pear boxes than in either Rabbit holes or Nettle beds !

Growth Rates

Growth rates were analysed by comparing the slopes of regressions of T.H.B. and weight (pooled for all chicks within a group) against chick age, using analysis of covariance. This was performed using the SPSSX MANOVA package (Anon. 1988). The data were visually examined to check that in no group did any individual chick contribute more than 20% of the data. This was appropriate for growth between 5 and 25 days post-hatch, as growth was found to be linear at this time (correlation coefficients ranged from 0.96 to 0.97 for weight and 0.98 to 0.99 for T.H.B.).

CHAPTER 3

THE DIET OF THE HERRING GULL

AT SANDA AND WALNEY

INTRODUCTION

Herring gulls exploit a wide range of prey types (Harris 1965, Spaans 1971, Hunt and Hunt 1975, Verbeek 1977, Pierotti and Annett 1986) and this has been widely interpreted as a reason for their success and dramatic increase during this century (Parslow 1967, Harris 1970, Verbeek 1977, Lloyd *et al.* 1991). In particular, the availability of Human refuse around colonies has been widely implicated in allowing population growth (Parslow 1967, Harris 1970, Spaans 1971, Mudge 1976) and increased breeding success in gulls (Hunt 1972, Mudge 1978). Other sources of food that have been newly exploited during the period of the Herring gull's dramatic increases in the British Isles have included; offal from fishing boats (Hudson *et al.* 1988), sewage and fish processing effluents (Hunt and Hunt 1975), waste from sewage sludge boats (Monaghan and Zonfrillo 1986) and fish docks (Harris 1965, Vermeer 1977). This increased food availability is thought to have allowed the Herring gull population to increase as a result of both increased survival outside the breeding season (Monaghan 1976), and increased breeding success (Spaans 1971, Mudge 1978). Food availability around breeding colonies has been shown to positively influence breeding success in Larids, through its effects on: timing of breeding, clutch size, clutch volume, egg volume, chick survival, growth rates, fledging weight and level of conspecific predation (Hunt 1972, Veen 1977, Pierotti 1982, Murphy *et al.* 1984).

Examinations of the diet of individual pairs within colonies have revealed that the observed wide range of prey types exploited by a colony of Herring gulls, is actually the result of pronounced differences in prey selection between pairs, with individual pairs specialising on rather restricted diets (Harris 1965, Davis 1975, Pierotti and Annett 1986). These specialisations on particular prey types (Pierotti and Annett 1986) or prey sources (Davis 1975) have been found to correspond with differences in breeding success between pairs (Davis 1973). Pierotti and Annett (1986), studying the diet of Herring gulls at Great Island, Newfoundland, classified specialist pairs as those where over 75% of ten or more

prey items were of one type. They found that over 80% of pairs in each of two breeding seasons, specialised on either refuse, mussels or Leaches Petrels (*Oceanodroma leucorhoa*). They found that these different specialists were consistently different in breeding success at all stages of reproduction studied; laying date, clutch size, clutch volume, hatching success, chick survival and fledging success. This led them to conclude "that individual variation in diet can be correlated with individual differences in fitness" (defining fitness in this case as fledging success per breeding bout).

Food availability and choice appear to affect breeding success both between breeding seasons and between pairs within a breeding season. For this reason, I studied the diets of Herring gulls at both Sanda and Walney, to establish what food types were important at each colony, and to establish whether changes in food availability around the colonies could explain the observed differences in the pattern of population change at each colony. While the diet of Herring Gulls has not been previously studied on Sanda, the foraging behaviour and diet of Walney Herring gulls has been extensively studied (Schaffer 1971, Vermeer 1977, Sibly and McCleery 1983a). All of these studies were carried out before the recent decrease in the number of pairs breeding at Walney. For this reason, a comparison of the diet between these two periods, was made to detect any major shift in diet as a result of any prey types becoming less available, and possibly to explain why the Walney colony has undergone such a dramatic decrease.

MATERIALS AND METHODS

Adult diet

Adult diets were assessed using a combination of pellets (regurgitated undigestible material) and other food remains (e.g. crab shells or fish bones), around the nest site (following Harris 1965, Spaans 1971, Pierotti and Annett 1986). The usefulness of pellet analysis in accurately assessing diet is limited (see for example Johnstone *et al.* 1990),

however Spaans (1971) assessed it as follows, "because the proportion of indigestible material is not the same for all kinds of food, this method does not indicate the ratio in which the prey species occur in the diet; its main usefulness is for the study of differences between areas or changes in the composition of the diet". As the main aim of this section was to compare the diet of Herring gulls between two colonies, this technique was considered appropriate.

All remains were collected from within 5 metres of study nests at 3 day intervals between the laying and hatching of the first egg. On Sanda, remains were collected from 187 nests. At Walney, a sample of 60 nests that were not involved in any experimental procedures were sampled in this way. All remains collected during the first visit after clutch initiation were not included in analyses. This avoided any bias in diet assessment that could result through the increased recording of resilient prey remains e.g. crab carapaces, and under-recording of less resilient prey remains e.g. pellets of fine fish bones. Remains were placed in self-sealing plastic bags and analysed in the laboratory. This involved teasing apart pellets with forceps, and recording the type of prey making up the bulk of the pellet. Where appropriate, the second largest component of the pellet was also recorded.

Following Andersson (1970), I examined pellets that consisted totally of grass under a dissecting microscope, to establish the presence of invertebrate remains, particularly the chaetae of earthworms.

Chick Regurgitates

Regurgitates were recorded during the routine weighing and measuring of chicks to study growth rates. All chicks handled for this purpose were also examined prior to weighing to find whether chicks had food in their proventriculus. If this was the case, the chick could

be encouraged to regurgitate the food by gently massaging it back up the oesophagus until the chick would voluntarily regurgitate (following Hunt 1972). In most cases where a chick was handled while the proventriculus contained food, the chick would regurgitate without any encouragement of this sort.

Regurgitates were mostly identified in the field. This was achieved by gently teasing apart the bolus with a match or suchlike and examining the contents. Regurgitates that were difficult to identify in the field were collected and identified later. Where identification in the field was possible, regurgitates were left near to the nest so that returning adults could re-eat them and then regurgitate them for the chicks. Observations away from the nest confirmed that this did occur.

When more than one chick from a brood regurgitated, there was no difference between chicks in composition of the regurgitates. As more than one chick is usually fed each time a brooding adult regurgitates food, it is likely that each chick would be regurgitating food presented from one foraging trip by an adult. For this reason, regurgitates from a brood were considered not independent, and treated as a single record for analysis.

Regurgitates of fish were examined for sagittal otoliths or characteristic fins or markings. After examination of many regurgitates nearly all were found to contain only fish flesh, and not whole fish. They were therefore mostly impossible to identify (except for sand-eels which were easily identified by their size, shape and "feel" in regurgitates). Fish regurgitates were therefore split into sandeels and non-sandeels (Fish spp.) for analysis.

In synchronously nesting birds, it is difficult to interpret apparent changes in diet with chick age as these may simply reflect changes in prey available to foraging adults. To control for these effects, chick regurgitate data for both colonies were split into two periods; before and after, the median hatching date of chicks that regurgitated (median hatching date of

chicks that regurgitated was chosen to ensure that roughly equal numbers of regurgitates were in the two periods). At Sanda the median date was June 4th and at Walney, June 1st. The composition of the diets were then compared between the two periods to find any differences that may have been the result of seasonal change in food abundance.

RESULTS

Adult diets at Sanda and Walney

The results of the pellet and food remains analysis at each colony are presented in Table 3.1. Incubating gulls on Sanda relied more on food from agricultural land than did those on Walney, with a higher proportions of grass and grain in their food remains. Of a sample of 20 pellets from Sanda that consisted of only grass, all were found to contain the chaetae of earthworms. This was also true of a sample of 12 grass pellets from Walney. The grain found in pellets was identified as Barley (*Hordeum distichum* or *H. polystichum*) at both sites.

On Walney, refuse made up a much higher proportion of the diet than at Sanda. Walney adults fed more on fish than those at Sanda, and the pattern of occurrence in pellets was also different; where fish were recorded in pellets from Sanda they were more often recorded as secondary prey than in pellets from Walney (Table 3.2). No difference was found in the relative occurrence of crabs between Walney and Sanda but, as with fish, the pattern of occurrence was different, crabs being recorded more as primary prey at Sanda than at Walney (Table 3.3). There was also a difference in the species of crab that gulls ate at Sanda and Walney, with gulls at Walney feeding mostly on species available in the inter-tidal areas of Morecambe Bay, while the gulls at Sanda fed mostly on species that normally live away from the inter-tidal zone and are not normally available to foraging gulls (Table 3.4).

Table 3.7 - Composition of chick regurgitates for chicks hatched on or before June 1st (period 1) and after June 1st (period 2), Walney 1990.

	Number of Regurgitates	
Food type	Period 1	Period 2
Fish spp.	32 (43.2%)	18 (26.4%)
Refuse	23 (31.1%)	26 (38.2%)
Earthworms	13 (17.6%)	10 (14.7%)
Marine molluscs	2 (2.7%)	6 (8.8%)
Unidentified	2 (2.7%)	6 (8.8%)
Other	2 (2.7%)	2 (2.9%)
TOTAL	74	68

Comparison of occurrence of prey types between periods;

Fish spp. - X^2 with Yates' correction = 3.74, 1 d.f., N.S.

Refuse - X^2 with Yates' correction <0.1, 1 d.f., N.S.

Earthworms - X^2 with Yates' correction <0.1, 1 d.f., N.S.

Table 3.1 Adult diet during incubation at Sanda 1989 and at Walney 1990.

	Sanda 1989		Walney 1990	
Prey type	Occurrence	(%)	Occurrence	(%)
Grass	233	(68.7)	26	(7.1)
Grain	64	(18.9)	13	(3.5)
Crab	23	(6.8)	24	(6.5)
Marine molluscs	7	(2.1)	54	(14.7)
Various	6	(1.8)	16	(4.4)
Fish	2	(0.6)	39	(10.6)
Refuse	1	(0.3)	133	(36.2)
"stones"	0	-	53	(14.4)
Unidentified	0	-	8	(2.2)
TOTAL	336		366	

Comparisons of occurrence of prey types between colonies;

Grass - X^2 with Yates' correction = 275.52, 1 d.f., $P<0.001$

Grain - X^2 with Yates' correction = 43.92, 1 d.f., $P<0.001$

Crab - X^2 with Yates' correction = 1.79, 1 d.f., N.S.

Marine molluscs - X^2 with Yates' correction = 85.58, 1 d.f., $P<0.001$

Fish - X^2 with Yates' correction = 6.95, 1 d.f., $P<0.05$

Refuse - X^2 with Yates' correction = 144.84, 1 d.f., $P<0.001$

Figure 3.3a Occurrence of terrestrial invertebrates in regurgitates of chicks of different ages, Sanda 1989.

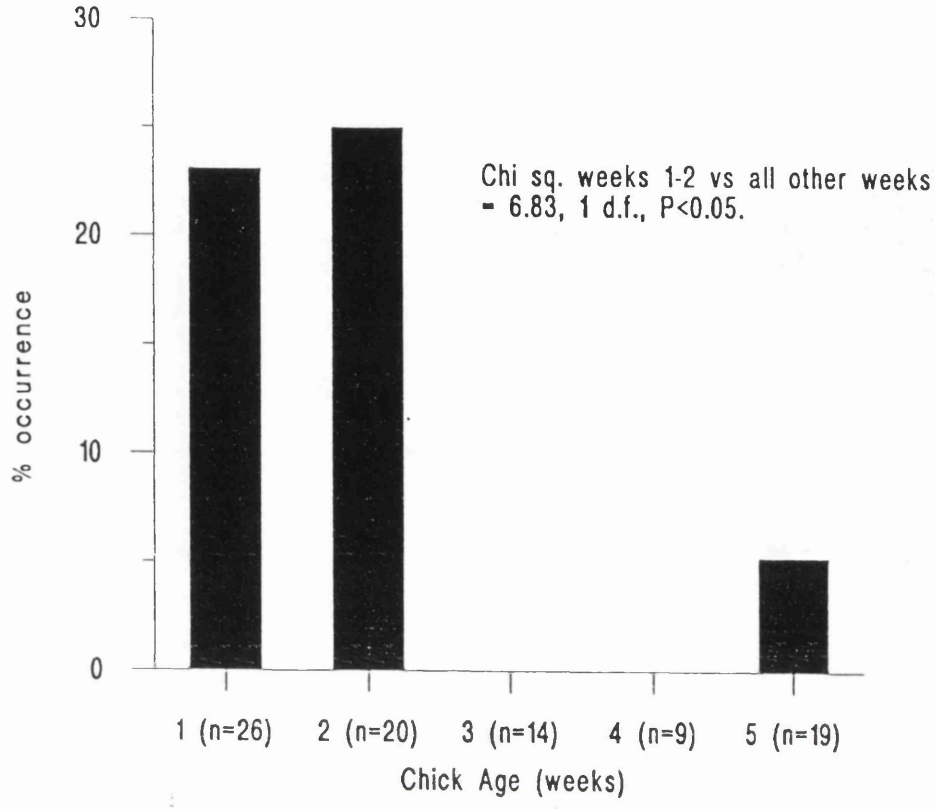


Figure 3.3b Occurrence of terrestrial invertebrates in chick regurgitates, Walney 1990.

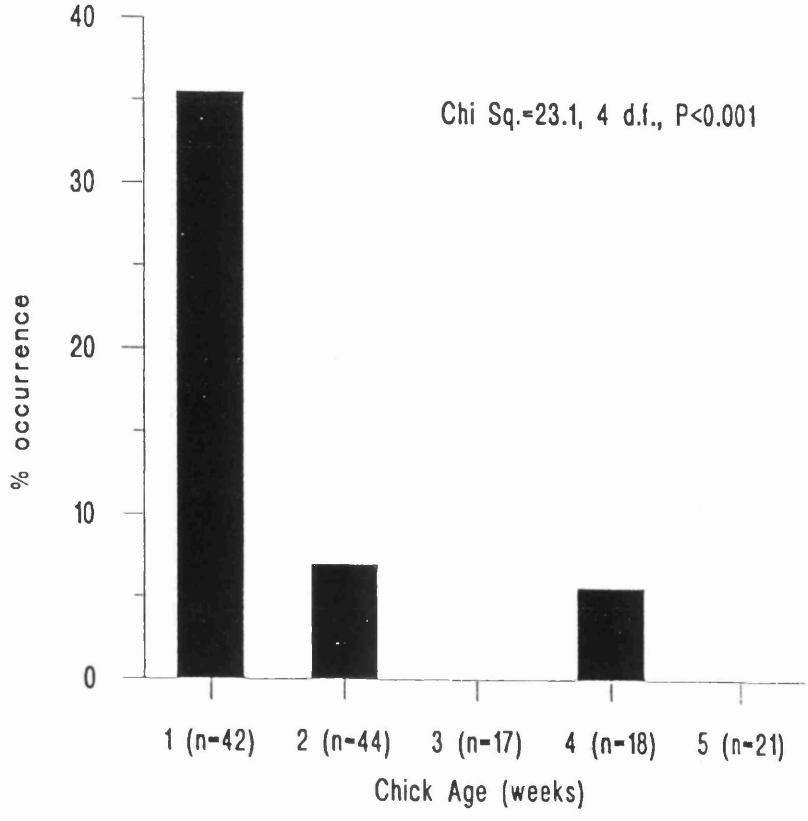


Figure 3.3c Occurrence of sandeels in regurgitates of chicks of different ages, Sanda 1989.

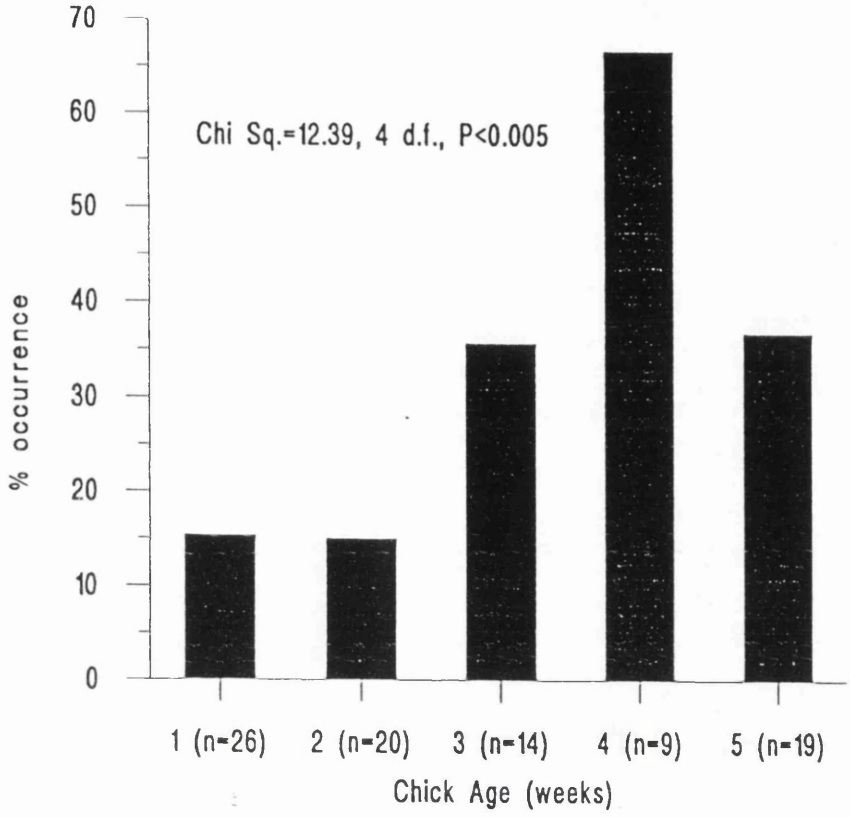


Figure 3.3d Occurrence of refuse in regurgitates of chicks of different ages, Walney 1990.

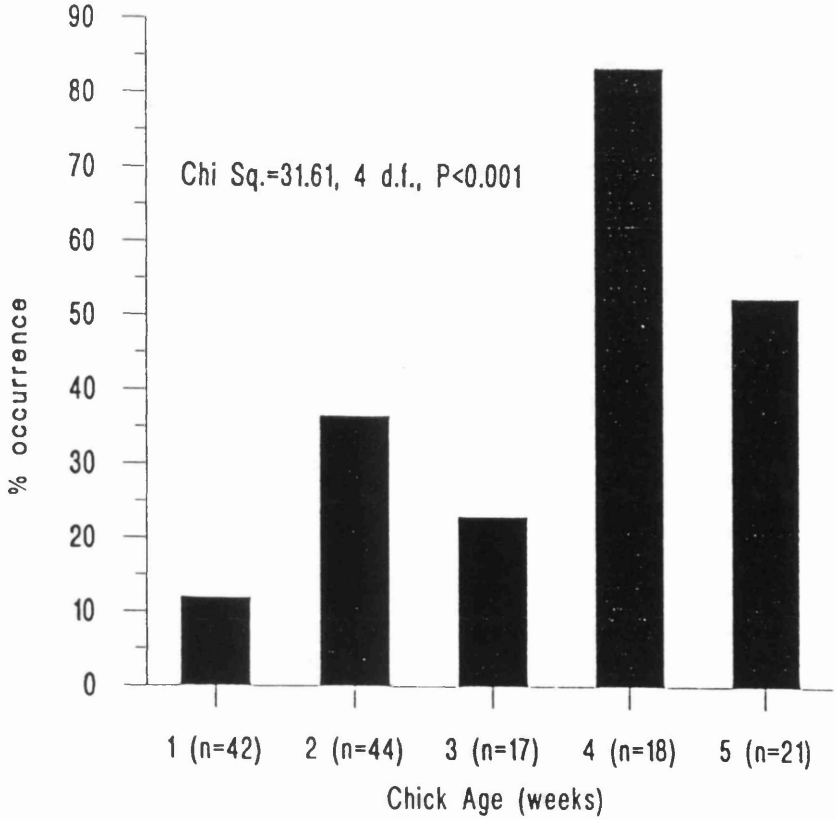


Figure 3.3e Occurrence of Fish spp. in regurgitates of chicks of different ages, Sanda 1989.

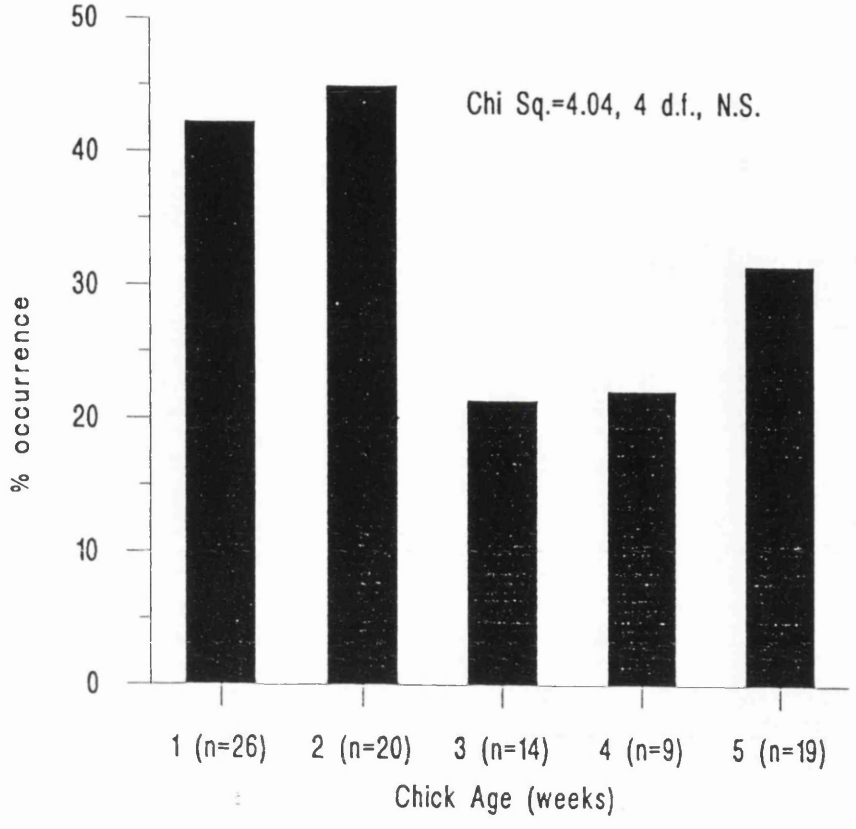
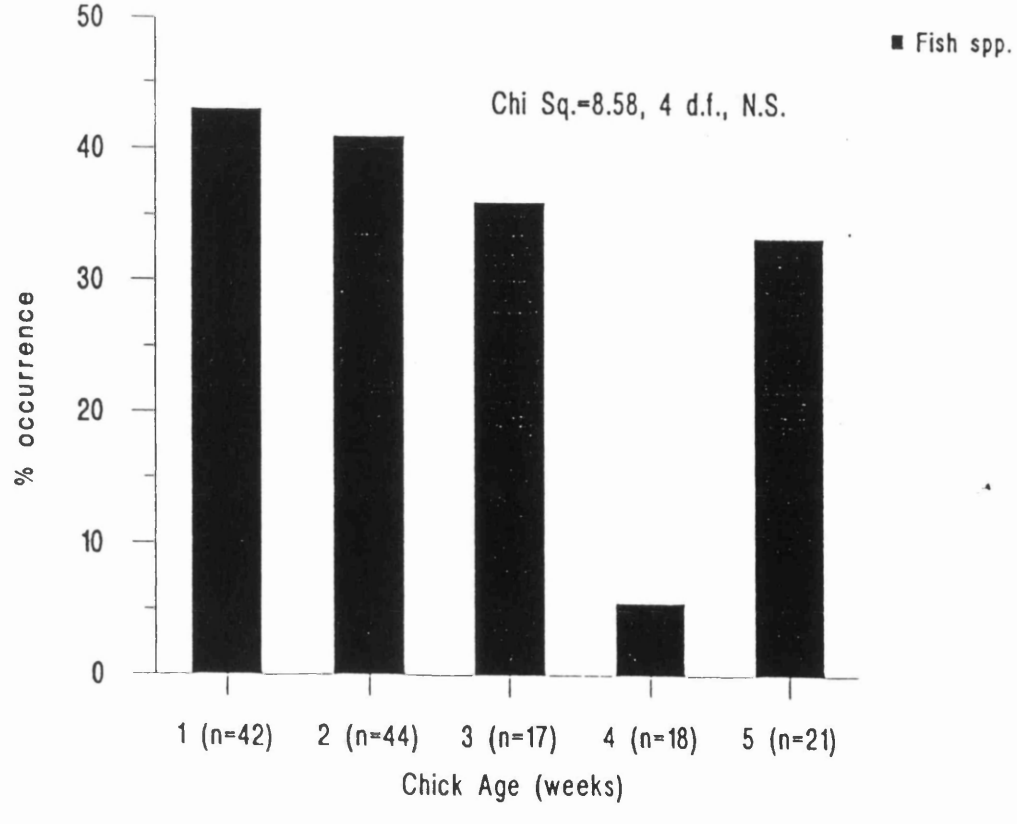


Figure 3.3f Occurrence of Fish spp. in regurgitates of chickis of different ages, Walney 1990.



or Walney (Figure 3.3f).

DISCUSSION

Food from agricultural land

Incubating Herring Gulls at Sanda rely on food from agricultural land much more than those from Walney. Grass and Grain were the primary component in nearly 90% of all pellets from Sanda whereas on Walney they accounted for just over 10%. Food from agricultural land was less important in chick diets; however it formed a large part of the diets of chicks less than 1 week old at Walney, and less than 2 weeks old at Sanda. The difference between colonies in the importance of food from agricultural land, does not appear to be a result of differences in availability. Gulls at Walney have access to more pastureland than do those from Sanda. Two factors however may influence the relative importance of agricultural land at the two colonies; firstly, gulls breeding at Walney have other major food sources available i.e. Walney refuse tip, Morecambe Bay and the fish-halls at Fleetwood. Second, there are a lot more gulls breeding at Walney than at Sanda, which may result in the availability of prey from agricultural land being more depleted than around Sanda. The total usage by gulls per unit area of land may be the same or higher than at Sanda, but this could still result in food from pastureland forming a smaller part of the diet of individual gulls.

The finding that the grass pellets examined under a dissection microscope contained chaetae of earthworms, confirms the findings of Andersson (1970), that grass pellets represent a diet of earthworms. Gulls were often seen feeding in fields around the South end of Kintyre, both following the plough and foraging on pastureland. During ploughing, flocks of several hundred gulls normally assembled in the fields and were seen feeding either directly behind the plough, or on freshly ploughed areas. These gull were probably feeding on invertebrates particularly earthworms. Large numbers of gulls were also seen feeding in freshly sown fields of Barley. On permanent pastureland, gulls did not gather in

the large numbers associated with ploughing or sowing activities, however gulls were always present during early morning and in the evenings. Around Walney, gulls were often seen in pastureland, particularly at high tide, early in the morning and after rain. At both Sanda and Walney, gulls feeding on pastureland employed two feeding strategies; walking and picking up items of food, or paddling the ground to bring earthworms to the surface.

Vermeer (1977), suggested that grain in the diet of Herring Gulls feeding around the Walney area had come from cattle cake, however in this study that did not appear to be true. Grain in cattle cake is normally crushed (*pers. obs.*). This was not the case with grain in the diets of gulls at either Sanda or Walney. On Kintyre, I observed gulls feeding on Barley as it was being sown, or in freshly sown fields. I did not see this at Walney, however it seems the most likely source of whole grain Barley.

Food from the inter-tidal zone/shoreline

The Walney gulls were found to rely heavily on food gathered from Morecambe bay ("stones", molluscs and crabs), both for adult diet during incubation, and chick diet. Gulls at Sanda do not have large inter-tidal areas available for foraging, so the finding that this part of the diet was far less important is not surprising. In spite of the differences in availability of inter-tidal areas in which to forage, crabs formed a similar proportion of adult diet at the two colonies. The species composition of the crab component of the diet at each colony shows that the sources of these crabs were however very different. Gulls at Walney fed mostly on the shallow-water dwelling *C. maenas* and *C. pagurus*, while those from Sanda fed more on deep water crabs *M. pipus* and *H. araneus*. These deep water species are not normally available to foraging Herring Gulls, and were probably discards from dredge trawlers fishing for *Nephrops norvegicus* or from a recently developed fishery in the Clyde for *M. puber*. Conversely, *C. maenas* and *C.pagurus* both feed in the inter-tidal zone and are therefore accessible to foraging gulls (Schaffer 1971, Vermeer 1977). Only one deep water crab was found in the crab remains at Walney, a single specimen of

H. araneus. From the species composition of the crab diets at the two colonies, it appears that the gulls at Walney feed on crabs they catch in Morecambe Bay, while the gulls on Sanda rely more on discarded crabs collected from behind dredge trawlers.

Fish

Most chick regurgitates of fish were of incomplete fish, particularly blocks of muscle. These bits appeared to come from fish too large for Herring gulls to catch themselves, particularly at Walney. The remains of fish in pellets also suggest this as they were often from very large fish e.g. on 2 occasions I found the rear spines of Spiny dogfish *Squalus acanthias*. These spines were from 3-year old fish (aged by counting the number of layers of enamel) which would have been at least 60cm long (P. Meadows *pers. comm.*) Vermeer (1977), showed that Herring gulls from Walney obtained large amounts of fish from Fleetwood fish docks. This would explain how Herring gulls could obtain such large fish, although they could also be obtained from scavenging along the tideline.

At Sanda, the non-sandeel component of the chick diet and the fish in the adult diet during incubation, were probably obtained from foraging behind Norway Lobster boats as, the size of the fish was often too large for gulls to have obtained by plunge diving. Norway Lobster boats fishing around Sanda often attracted very large numbers of Herring gulls. Flocks normally consisted of 2-300 birds while the nets were being pulled in, however on several occasions flocks of over 500 birds were seen and on one occasion the flock was estimated to be around 1200 birds.

At Walney, Vermeer (1977) found that the main source of fish in Herring gull diets was Fleetwood fish docks, and it seems probable that this is still the major source of fish in view of the large size of fish recorded. The fish eaten by gulls at Sanda are probably caught by the adults themselves or obtained as discards from Norway Lobster boats, the discards from which are smaller than those from whitefish trawlers (Furness *et al.* 1988) and also presumably from fish docks. As these are on average smaller than those

obtained by gulls on Walney, they will be more likely to be recorded as secondary rather than primary prey. The finding that in adult diets fish were recorded mostly as primary prey at Walney and secondary prey at Sanda offers support for this hypothesis. Furness *et al.* (1988), found that these smaller discards were more suitable for Herring gulls than the larger discards from whitefish boats, as Herring gulls were able to swallow them quickly and thus avoid klepto-parasitism from other species.

At Sanda, sandeels were caught by 2 methods; firstly, adults would participate in large mixed-species feeding flocks around Sanda when sandeel "balls" were located. Adults would then either plunge-dive from the air, or from a sitting position on the surface to capture the sandeels. The second source of sandeels was through klepto-parasitism of other seabird species. During observations at auk colonies on Sanda and Sheep Island, I often saw Herring gulls sitting amongst brooding Guillemots and Razorbills. These birds would wait for incoming auks and force them to drop any fish they were carrying back for their chicks. After observing this for several hours, I became convinced that this was a strategy employed by individual gulls and not simply a few interactions I had happened to see by chance. In particular, one bird with partial oiling of the breast feathers (and therefore easily recognisable), would sit at the same point in a Razorbill colony between days, and on several occasions I saw it leave after successfully robbing Razorbills of sandeels, and return to the same spot roughly 15 minutes later. This bird was seen to defend "it's" area of Razorbills against intruding Herring gulls, as were many other gulls which also appeared to be holding feeding territories within the auk colony. Ingolfsson (cited in Cramp and Simmons 1983) observed individual Herring gulls defending rafts of Eiders for the purpose of food stealing; however I can find no reference to Herring gulls defending any other species in this way.

Refuse

Refuse was the most prevalent prey type in the diets of incubating gulls at Walney, and accounted for over a third of chick regurgitates. In stark contrast refuse formed less than

5% of the diet of both adults and chicks at Sanda. However, at Sanda, gulls have no opportunity to feed at refuse tips such as the one at Walney, so this result is of no great surprise.

Changes in availability of diet - Sanda.

Herring gulls at Sanda exploit 3 main food sources; agricultural land, Norway Lobster boats and sandeels. No previous studies have been made of the diet of Herring gulls nesting on Sanda or any other Clyde Sea colonies. It is therefore difficult to assess changes the relative importance of these prey types. It is however possible to tell by indirect means, whether the availability of each of these food sources has increased over the period of increase in Herring gulls at Sanda.

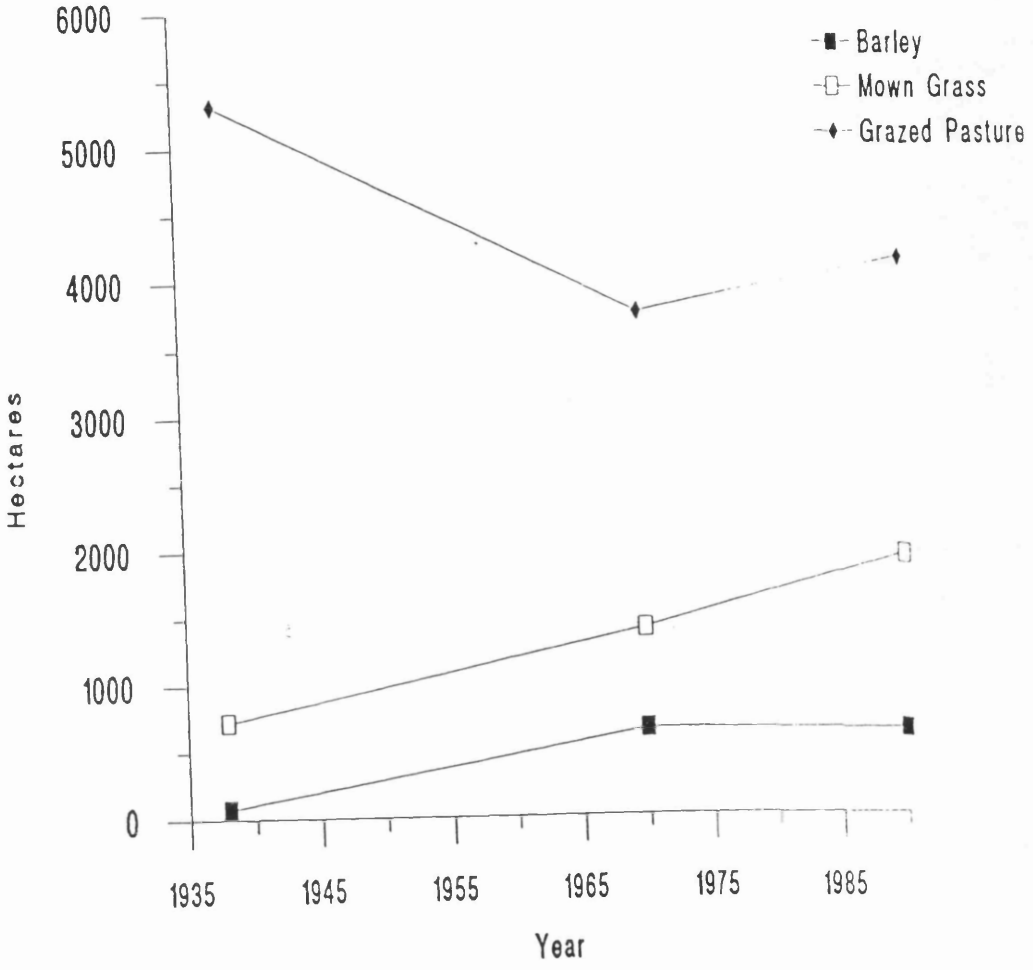
Agricultural land

Data on the areas of land used for growing different crop types in each parish are collected annually by the Scottish Office Agriculture and Fisheries Department (SOAFD). Using these data for the parishes of Southend and Campbeltown (covering all land within 30 miles of Sanda) for 3 years spanning the period of increase of Herring gulls at Sanda, 1938, 1970 and 1990, we can see the changes in the areas of land used for the growing of crops that are exploited by Herring gulls i.e. barley, permanent grazing and grass production for sileage manufacture (Figure 3.4).

The area used for growing Barley increased substantially between 1938 and 1970, from 74.3 hectares to 646.1 hectares, with a subsequent slight reduction to 633.9 hectares by 1990. The amount of permanent pasture has decreased during this period from 5309.7 hectares in 1938 to 3749.7 hectares in 1970 and 4137.2 hectares in 1990. The area of land used for growing "mown grass" i.e. for sileage production, has increased dramatically from 723.9 hectares in 1938 to 1398.7 hectares in 1970 and 1942.1 hectares in 1990.

Of these types of agriculture, the growing of Barley and of grass for sileage appeared to be

Figure 3.4 Changes in the areas of land used for grazing, sileage production and for growing Barley, in the parishes of Southend and Canpbeltown, Argyll, between 1938 and 1990.



far more important to foraging gulls than the areas of permanent pasture. Both provided opportunities for gulls to feed while the fields were being ploughed, which allowed gulls access to large numbers of terrestrial invertebrates, and in the case of Barley, the subsequently planted seed was also an important food source.

The amount of land used to grow crops that were the source of most of the food for adults during incubation, and a high proportion of the diet of chicks during the first 2 weeks post-hatch, has increased substantially during the period of population growth at Sanda.

Food from fishing boats

The total tonnage of fish caught in the Clyde Sea area has declined since the 1970s (Hislop 1986). It would appear then that the opportunity to feed on discards and offal has declined, however there are reasons to believe that this is not so.

The reason for the reduction in the tonnage of fish landed in the Clyde has been the spectacular decline in the numbers of Herring (Hislop 1986). However, Herring gulls are relatively unsuccessful at foraging behind trawlers catching whitefish or Herring, (Hudson 1988, Furness *et al.* 1988). From my observations and from the composition of the crab component of adult diet and the relative occurrence of fish as secondary prey in pellets, it appears that Norway Lobster boats are far more important to the gulls at Sanda than are Herring or other fishing boats. During the period of increase in Herring gull numbers on Sanda, the Norway Lobster fishery has opened and grown dramatically on the Clyde. The fishery for *N. norvegicus* developed during the mid 1960's and by the mid 1980's over 1500 fishing trips for Nephrops were taking place in the Clyde annually (Hislop 1986), making the fishery for Norway Lobsters the most important in the Clyde (Furness *et al.* 1988). Since then, the fishery has further increased, and fisheries for *M. pipus* and *C. pagurus* have also become important; 27.7 tonnes of the former were landed in the outer Clyde Sea area during 1984 (Mason and Fraser 1986). Unlike the other fisheries in the Clyde,

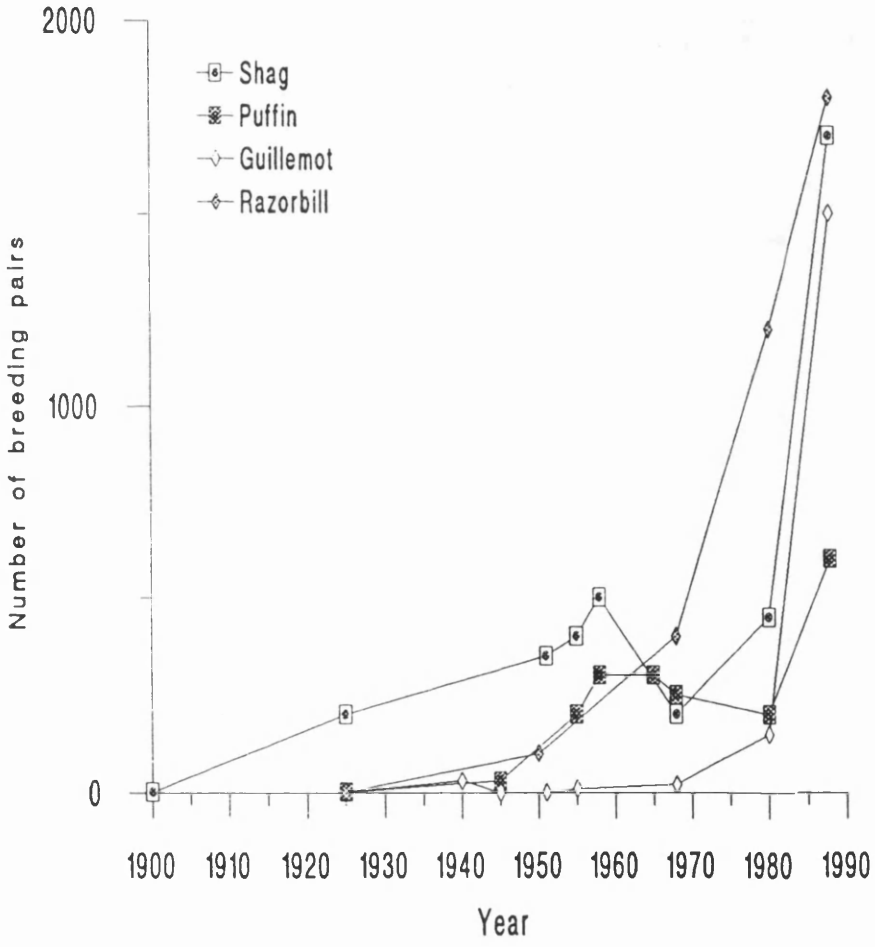
the main season for *Nephrops* and crabs, is during the Herring gull's breeding season, running from April to November, with a peak around July-August (Hislop 1986). This peak coincides exactly with the peak fledging time for Herring gulls.

The availability of food from Norway Lobster boats has increased substantially over the same period in which Herring gulls have increased on Sanda. This fishery has only started since the increase in Herring gulls had already started and cannot therefore be implicated in having facilitated the initial increase. However, from the apparent prevalence in the diet of both chicks and adults, it appears that this extra food source is certainly an important addition to the foraging opportunities available to Herring gulls at Sanda and may have helped sustain the growth of the Herring gull population since the 1960's, the period of most rapid growth.

Sandeels

The populations of sandeels in the Clyde have not been studied; however there is circumstantial evidence from the changes in numbers of other species of sandeel-feeding seabirds around Sanda, to suggest that the availability of sandeels has dramatically increased around Sanda in recent years. During the summer of 1988, I studied the diets of several species of seabirds at Sanda by either observation of adults returning with fish in their bills (Razorbill, Puffin and Guillemot), or from chick regurgitates (Shag). Of these all but Guillemot were found to feed mostly on sandeels; Shag 100% (n=472), Razorbill 99.6% (n=1148), Puffin 99.7% (n=385) and Guillemot 31.7% (n=202) (details published in Morton 1989). This reliance on sandeels does not appear to have been due to their presence in unusually large numbers in 1988, as in 1988 I did not see the large concentrations of seabirds feeding on sandeel "balls" that I did in 1989. The populations of all of these species have increased substantially coincidental to the increase of Herring gulls at Sanda (Figure 3.5). The dramatic increase in the numbers of these species suggest that their main prey, sandeels, have become increasingly available to seabirds around Sanda.

Figure 3.5 Changes in breeding populations of 4 species of seabird nesting on Sanda from 1900-1990.



It is possible that these increases have resulted from the cessation of human persecution of these species. Gibson (1969), however makes no mention of human exploitation or control of these species around Sanda, and with all of these species, the nests are mostly difficult to reach being sited mostly in crevices in boulder beaches. The most important nesting areas for Razorbill and Guillemot are in inaccessible stretches of coast on Glunimore and Sheep Island making human exploitation even more difficult. It therefore seems unlikely that the increases in these species are due to any reduction in human persecution, but that they strongly suggest that the availability of sandeels has increased concurrent with the increase in Herring gulls and other seabird species.

Changes in availability of diet - Walney.

Three studies of the foraging behaviour of Herring gulls at Walney have been made (Schaffer 1971, Vermeer 1977, Sibly and McCleery 1983a). Of these, none presented results of examination of pellets, so a direct comparisons of the findings is not possible. It is however possible to compare the general findings of each study.

Vermeer (1977) and Sibly and McCleery (1983a), found that the main feeding areas for Herring Gulls were at refuse tips, in fish halls, harbours, and intertidal areas, which broadly agree with my results. These studies established the feeding preferences of Herring Gulls by a combination of counts in feeding areas, observation of "flight lines" (direction of flight of birds leaving the colony to forage), and radio-tracking. Neither study presented data on the composition of the diet so a direct comparison with this study is not possible. The results of Vermeer (1977), Sibly and McCleery (1983a) and McCleery and Sibly (1986), however broadly support the findings of my food remain analysis, showing that the main prey types/sources for Herring gulls at Walney are; refuse, fish (mostly from Fleetwood docks), invertebrates from farmland in Furness, and inter-tidal organisms (from Morecambe Bay and probably also the Duddon Estuary). McCleery and Sibly

(1986) found that of 122 foraging trips made by 16 breeding gulls during the incubation period, the following foraging sites were used;

Morecambe Bay	35	(28.7%)
Walney Landfill Site	33	(27.0%)
Walney Mussel "skear"	19	(15.6%)
Fleetwood/Morecambe	19	(15.6%)
Farmland	16	(13.1%)

Combining these data into categories of food type gathered at each site e.g. Morecambe Bay and Walney Mussel skear, allows a comparison between the foraging patterns of Herring gulls at Walney in 1976 and with the diet results from 1990 (Table 3.8). Whilst there may be biases introduced in comparing the results of radio-tracking foraging birds and using prey remains to determine where birds are feeding, the close similarity between the results suggest that these are not serious. Pellet analysis under-records the presence of soft-bodied prey in diet analysis while over-representing prey that are relatively undigestible. In comparing between the three foraging areas, this should not introduce a bias if the number of pellets produced from each foraging area is the same for the same number of visits. In the case of the refuse tips, pellets contained a large amount of undigestible material and therefore one might expect more pellets to be formed from less visits to refuse tips than to the other two foraging areas. It appears however, that even gulls feeding on soft-bodied earthworms, ingest grass to allow pellet formation. This may result in the same number of pellets being formed per food source, regardless of the amount of undigestible material in each food type. If refuse-feeding gulls do produce pellets more often than birds feeding elsewhere, then this would result in refuse pellets being over-represented in the diet, and that the similarity between my findings and those of McCleery and Sibly (1986) represent a decrease in the actual usage of refuse tips by foraging gulls.

Table 3.7 - Proportion of Herring Gulls feeding on different prey types/sources during incubation at Walney in 1976 and 1990

Prey source	1976*	1990**
Farmland	16	39
(%)	(13.1)	(11.4)
Inter-tidal	54	131
	(44.3)	(38.3)
Man-made	52	172
(Refuse and Fish)	(42.6)	(50.3)
TOTAL	122	342

X^2=2.121, 2 d.f., N.S.

* Data from McCleery and Sibly (1986). Records represent visits of radio-tagged birds to feeding sites.

** Data represent the type foraging sites as determined by the dominant type of prey in any one pellet/prey remain.

was the "preferred" prey as measured by the amount of time radio-tagged gulls spent feeding on refuse divided by the amount of time for which refuse was available. Birds spent a lower proportion of available time feeding on earthworms (27.6% of the time available), than on either inter-tidal invertebrates (41.8%) or refuse (56.7%). Using the rate of weight gain from birds feeding on different foods, knowing the availability (hours each day when each food type was available to foraging gulls) of each food type and energetic value of these foods, Sibly and McCleery (1983b) showed that if Herring gulls at Walney did not have access to refuse, then they would not be able to achieve a high enough rate of energy intake to survive.

In view of the fact that the Herring gull population at Walney has decreased, and that refuse is by far the most important food type to nesting birds at Walney, the finding that refuse forms a similar proportion of the diet as before the decline is remarkable. If availability of refuse had not changed, then one might expect the proportion of refuse in the diet to have increased as this is the preferred food type and competition from conspecifics should have decreased. That it forms the same proportion of the diet, suggests that competition has remained at approximately the same level. If the number of gulls breeding at Walney is dependent on the amount of refuse tipped locally, then one would expect the proportion of refuse in the diet to have remained the same between the this study and that of Sibly and McCleery (1983a). If the population was controlled by some other factor, then one would expect the proportion of refuse in the diet to have increased unless the population decrease had coincided exactly with a decrease in refuse availability.

Although information on the amount of tipping is not available for the initial years of the decline in the Herring gull population at Walney. Data are available for the

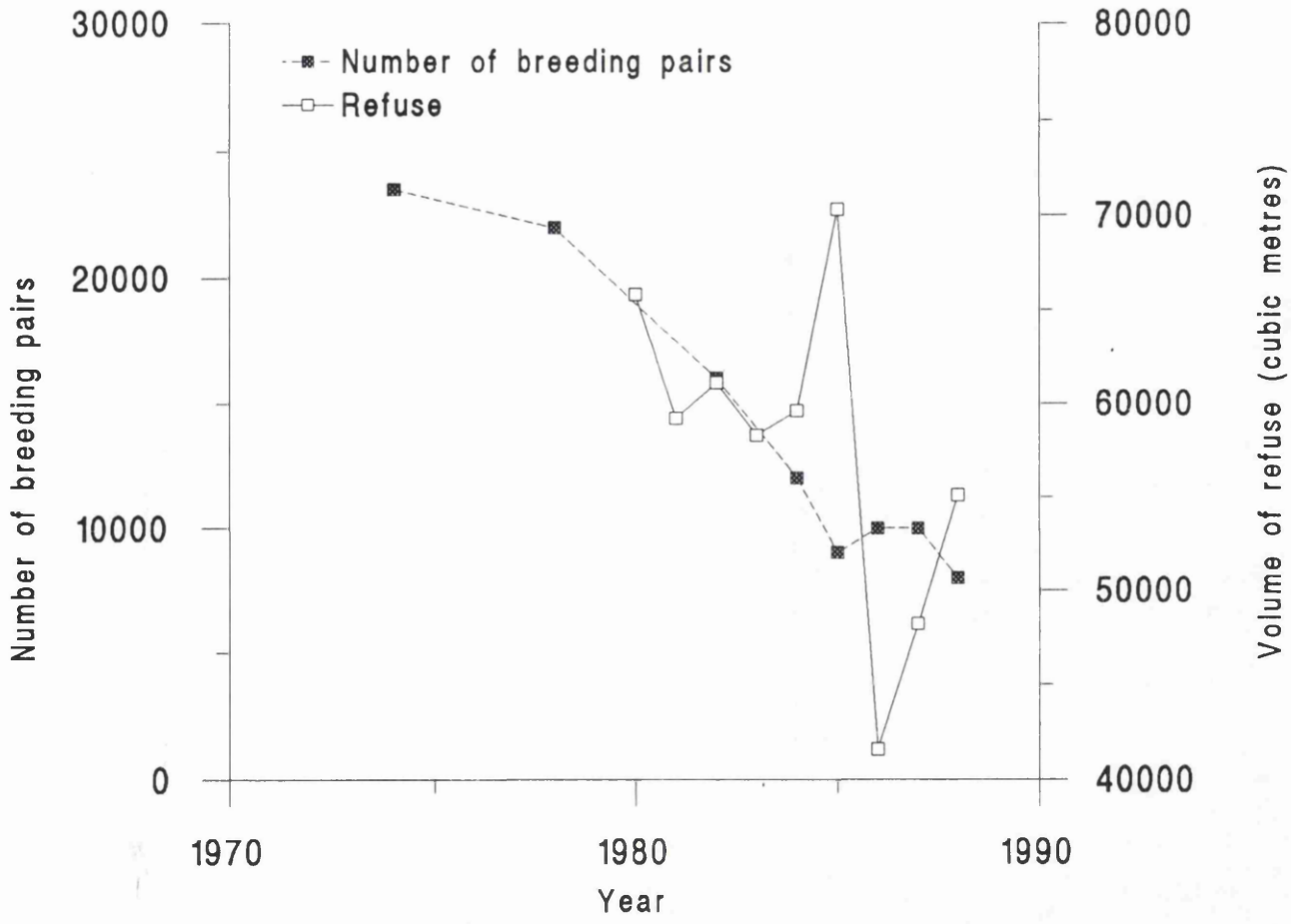
years in which the decline was most rapid (but only for Cumbria). The total volume of domestic refuse tipped at landfill sites around Walney, has declined during the period of most rapid decline of Herring gulls (Figure 3.7a-3.7c). This is true of the Walney tip itself, and tips within 25km and 50km of Walney i.e. all tips within reasonable flying range (Vermeer 1977). The decline in tipping appears less dramatic than the decline in the population of gulls. The more rapid decline in the gulls could be the result of a decrease in the absolute volume tipped, and some change in tipping practise. Rod Leather (head of refuse disposal for Cumbria County Council), believes that a major change over the period has been that refuse is now covered with top-soil or other refuse more quickly than during the 1970's or early 1980's. This would result in gulls losing foraging opportunities and the amount of food gulls could obtain per unit volume of refuse.

It seems unlikely that their could have been any sufficiently large decreases in prey availability from Furness farmland and Morecambe Bay, to account for the dramatic decline in the gull population at Walney. The area of pastureland in Furness is limited to the low lying coastal area. There is very little cereal production in the area, so it would appear that pastureland has not been lost to cereals. Morecambe Bay does not appear to have changed as a potential source of food, as no similar declines in populations of birds where there is some overlap in diets (e.g. Eider *Somateria mollisima* feeding on the Mussel *Mytilus edulis* (Cramp and Simmons 1977)), has been observed.

While the availabilities of earthworms and food from inter-tidal areas are not possible for me to assess, it appears unlikely that either has collapsed sufficiently to account for any change in the number of breeding gulls at Walney. Unfortunately, I was not able to get any information about the availability of food from Fleetwood docks. It seems unlikely that declines in availability food from these sources alone was important enough to account for any changes in population.

Schaffer (1971) studied the diet of a combined sample of Lesser black-backed and

Figure 3.7 The volume of refuse tipped at South Walney and the number of pairs of Herring gulls breeding at South Walney, 1970-1988.



Herring gull chicks at Walney. This combination of species makes a direct comparison of results inappropriate, as Vermeer showed that these two species feed in different locations around Walney. Lesser black-backed Gulls prefer to feed more at sea, in cities and in fields, while Herring Gulls feed more at refuse tips, fish halls and inter-tidal areas. The general findings of Schaffer's study and my own, are however similar. He found that chicks diets comprised mostly of fish (c29%), refuse (between 25 and 55% of the diet), and earthworms (27% during the first week post-hatch, <10% thereafter).

The similarity between adult diets found by Sibly and McCleery (1983a) and in this study, and between chick diets in Schaffer's (1971) study and this study, suggest that no real change in the relative abundance of the three main prey types, has occurred. As the absolute volumes of refuse tipped have declined, this suggests that competition fro refuse has remained the same as a result in the decrease in breeding Herring gulls at Walney.

Changes in chick diet with age

The finding that the composition of chick diet changes with chick age has been documented by several other authors (Schaffer 1971, Pierotti and Annett 1986). Of these studies, only Pierotti and Annett (1986) offered any evidence that the observed relationship between chick age and diet was not simply the result of changes in prey availability during the chick-rearing period. They showed that prey types fed to chicks of different ages were available before the chicks hatched and after chicks had ceased to be fed certain prey types. Their results are not however conclusive, as although prey types were present, the relative abundance of the prey types was not known. For example, they found that chicks "switched" diet to squid at about 3 weeks post-hatch even though squid had been caught for several weeks by boats fishing in the area. This does not exclude the possibility that the apparent "switch" did not occur as a result of squid numbers having increased to a level where there were enough to make foraging for them a viable option to the adult gulls. Their finding could also be the result of other prey types becoming less

available as the season progressed. The results from Sanda and Walney support their interpretation however, and it does appear that chick diet does change in relation to chick age rather than to changes in prey availability, as no difference in overall diet was found between chicks hatching in the first and second halves of the hatching period.

Schaffer (1971) studied the relationship between diet and chick age at Walney. However, as he collected regurgitates from both Lesser black-backed gulls and Herring gulls without attempting to identify their species, his results are not directly comparable with mine. He found that earthworms were important particularly during the first week post-hatch, after which time they were present in less than 10% of regurgitates (note that he recorded presence in a regurgitate rather than the dominant prey type in a regurgitate as I did). Refuse followed a similar pattern to that which I found, increasing until the chicks were approximately three weeks old and then declining again. Fish showed no change as the chicks grew, accounting for roughly 29% of chick diet throughout chick growth.

The reason for a change in chick diet with chick age is difficult to identify, as so little is known of the nutritional requirements and digestive abilities of wild birds, let alone the way that these change with chick age (Ricklefs 1983). The cause of the change may not be related to the nutritional requirements of the chick; they may be the result of changes in foraging constraints placed on the adult gulls as the chicks grow. Chicks during the first week post-hatch are particularly vulnerable, as a result of their poor thermoregulatory abilities and small size and poor motor abilities rendering them open to predation. This may result in adults having to brood and defend chicks more during the first week post-hatch. As a result, there may be less time available for adults to forage than when the chicks are older and capable of both defending themselves against predation, escaping predation and of efficient thermoregulation. Adults may therefore be constrained in the amount of time they can devote to foraging at this stage and this may be reflected in their "choice" of prey type.

The prey types fed to small chicks suggest that any changes in chick diet in relation to age, are in fact not the result of adults being constrained in the amount of time they can spend foraging. If adults were constrained in this way, then one would expect them to exploit the most profitable prey in terms of nutrients/energy per unit time. The observation that earthworms are fed to very small chicks does not support this. Sibly and McCleery (1983b) showed that gulls foraging for earthworms on pastureland around Walney had a far lower rate of energy gain than did those feeding on refuse. For observational evidence that adults are not constrained in the amount of time they spend foraging while the chicks are less than 1 week old, see Chapter 8.

The change in diet with chick age would appear then to be due to changes in requirements of the chick. These could be of two types; Firstly, chicks may require certain nutrients at certain stages of growth. Secondly, the abilities of chicks to process food may increase as the chicks grow. As so little is known of the nutritional requirements of chicks, it is not possible to determine whether these dietary changes may reflect the changing nutritional needs of chicks as they grow.

There are four main ways in which a chick's ability to process food could change with age: the size of prey that chicks can swallow, the amount of food they can store/digest at one time, their digestive ability and their ability to absorb digested material.

Unlike many species of bird such as birds of prey and some skuas (Furness 1987), gulls are not able to tear up prey before presenting it to chicks. The actual size of a prey item presented to a chick, is therefore very important. Many of the regurgitates from chicks older than 1 week, were far too large for younger chicks to swallow. The change in diets may simply reflect adults provisioning chicks with prey small enough for chicks to ingest. This would perhaps explain the high occurrence of earthworms during the first two weeks

On Sanda, I found a brood of 3 chicks that had apparently starved, that had next to them four piles of small (>2cm<4cm across the carapace) *Carcinus maenas*. Whilst it is impossible to be certain that the cause of death was starvation (although the gullets were completely empty), it seems likely that these chicks had died of starvation as a result of the adults presenting them with prey too large for the chicks to ingest.

Small chicks are not only limited in their ability to ingest large prey, but they also have a smaller crop, stomach and gut than older chicks. This means that they can process far less food at any one time than older chicks can, both in terms of the amount they can ingest and the amount they can absorb. The gut has been shown in altricial species to increase linearly as a proportion of body weight (Konarzewski *et al.* 1989); however Ricklefs (1983) has suggested that this relationship may not be true of precocial species, where high mobility is important and gut size is proportionally smaller in small chicks than in older chicks. If in gull chicks, gut weight does grow in proportion to body size, then the food required by small chicks must be more energy rich. This is because a small chicks surface area to volume ratio is much higher than that of a larger chick, and it must therefore maintain a much higher B.M.R. (Sibly and Calow 1986) Dunn (1978), has shown that chicks shortly after hatching, have a B.M.R. 2.5 times higher than that of older chicks.

The ability of different aged chicks to digest food has not been assessed (Ricklefs 1983); however there is circumstantial evidence to suggest that very young (< 1 week old) Herring gull chicks are not capable of digesting some foods that older chicks can. Spaans (1971), investigated the food requirements of growing chicks by feeding them a mixed diet of fish. He found that during the first week post-hatch, chicks suffered high mortality and ate far less than would be expected for their body-size. These chicks were kept in incubators so this high mortality would not seem to be due to the young chick's poor thermoregulatory abilities. As the chicks were fed *ad libitum*, it appears that the cause of death was the chick's inability to digest "whole" fish, not a result of lack of food. Older

chicks (> 1 week post-hatch), showed no similar mortality and appeared perfectly capable of digesting "whole" fish.

This finding suggests that "fish" is not a suitable diet for very small chicks, however at both Sanda and Walney, fish was a large component of the diet of chicks of all ages. This seemingly contradictory result could be explained if adults fed small chicks fish that were already partly digested. Unfortunately the state of digestion of prey was not recorded during regurgitate analysis however, Deusing (1939) reported that Herring gulls did feed young chicks with pre-digested fish. He believed that the older a chick was, the less digested the fish it was fed. There is a problem with this observation in that, small chicks may take food from one adult foraging trip, over a period of several hours. Older chicks are more capable of consuming the contents of an adult's crop in one meal. When food is left over after a feeding bout, adults re-ingest it until the chicks beg for further food. As the adults store this food in the proventriculus (Hunt 1972), which is an important source of digestive enzymes, it seems likely that after re-ingestion food will become more and more digested, and that this results from adults storing the food rather than the adults trying to pre-digest it for the chicks. With prey unsuitable without some predigestion, it may be that adults could store the food and regurgitate it at regular intervals until the chick "decides" that it is edible. It would be interesting to observe the state of digestion of prey on first presentation to chicks after an adult's foraging trip, to establish whether this pre-digestion is merely an artifact produced by longer storage of food, or a strategy employed by adults to make an otherwise unsuitable prey type acceptable to young chicks.

Schaffer (1971) also supported Deusing's findings when he interpreted changes in the diets of gulls chicks on Walney. He suggested that in the case of earthworms, "It seems likely that there are not too many foods that can be fed to very small gull chicks without much predigestion by the parent, so that earthworms, when available, may be one of the few foods that a young gull can handle from the first day of life". He also suggested this as an explanation for the low initial occurrence of insects and Prawns (*Leander serratus*) in

chick diets as chicks grew, and the absence of crabs and mussels during the first week post-hatch. In the case of the last two prey types, I feel that another important factor could be the ability of chicks to form pellets at an early age particularly to expel sharp pieces of shell and carapace. I noticed that in young chicks at both Sanda and Walney, regurgitated pieces of fish rarely contained bones that could potentially choke a chick, whereas fish from older chicks was far more boney. I also found a similar trend in the types of refuse that chicks were fed, with young chicks being fed less solid material than older chicks. While chicks were small, I noticed no small pellets on territories. I first noticed these when the chicks were over a week old. It would be interesting to establish whether young chicks are able to form pellets, and if not, at what age they develop this ability.

The reason for chick diet changing with age is not clear, there being evidence that small chicks are constrained in both the size of prey that they are able to ingest, and in their ability to digest prey that form the major part of the diet of older chicks. Adult gulls appear to alleviate the last problem by partly digesting fish presented to chicks; however observations of the state of digestion of fish presented to chicks by adults returning from foraging trips are required to ascertain whether this pre-digestion is merely the result of longer storage in the adult's proventriculus.

CHAPTER 4

FACTORS AFFECTING BREEDING SUCCESS WITHIN COLONIES: THE EFFECTS OF LAYING DATE, CLUTCH SIZE AND EGG VOLUME

INTRODUCTION

Natural selection produces individual animals 'designed' to maximise the number of their genes present in subsequent generations. Three of the most important ways in which an individual animal can maximise reproductive output are the time at which it breeds, reproductive rate and the amount of parental investment that goes into each breeding effort. In terms of egg production in the Herring gull, these can be loosely interpreted as timing of breeding, clutch size and clutch volume. Each of these affects the final outcome of an individual breeding bout:

Timing of breeding

Timing of breeding in gulls has been demonstrated to be inversely related to clutch size, clutch volume, hatching success, hatching weight and both pre-fledging and post-fledging survival of chicks (Paynter 1949, Parsons 1972, Parsons *et al* 1976, Hunt and Hunt 1976, Burger 1979). These findings are not restricted to the gulls; they have been found throughout many groups of birds (see Newton 1989). To understand why this seasonal decline in breeding success occurs one must first look at ultimate and then proximate factors controlling timing of breeding. Breeding is normally timed such that the time of peak food availability coincides with the time at which the chicks are growing and thus require most food (Lack 1954). This is certainly true of most altricial species, but in the case of the Herring Gull early fledging may also allow the young longer to acquire foraging skills required for them to survive times of food shortage post-fledging. These times of shortage could be the fledgling's first winter which Kadlec and Drury (1968) found to be the period of highest fledgling mortality, or late summer, when adults are at their lowest body weight, possibly as a result of breeding stress or food shortage (Coulson *et al.* 1983b).

If breeding is timed so that peak food availability occurs while the chicks are growing, then egg-laying must occur several weeks before the food supply reaches it's peak. The

proximate constraint on breeding at the optimal time is the ability to accrue sufficient reserves early in the season to allow the clutch to be laid in time to hatch before peak food availability. Thus, the usual explanation for the effect of timing of breeding on so many breeding parameters is that later breeding birds within a species are those individuals unable to accrue sufficient body reserves quickly enough pre-breeding to commence breeding at the same time as higher "quality" early breeders (Perrins 1970, Drent and Daan 1980, Ewald and Rohwer 1982,). The finding that later breeding birds breed comparatively less successfully than early breeders may therefore be due largely to "quality" rather than to the actual direct effect of timing.

Clutch Size

Current theories on the ultimate factors affecting clutch size are based on the work of David Lack. His original hypothesis was that breeding birds produce a clutch, the size of which will result in the greatest number of young surviving to breeding (Lack 1948, 1954). More recently this has been modified to take into account the effects of individual breeding bouts on lifetime reproductive success (Royama 1966), and his hypothesis may now be restated as "birds lay the number of eggs that results in the parents operating at the optimal working capacity" (Winkler and Walters 1983). This has been demonstrated in several species e.g. Starlings (*Sturnus vulgaris*), House sparrows (*Passer domesticus*), Red grouse (*Lagopus lagopus scoticus*) and Herring gull (see Perrins and Birkhead 1987 for references and further examples).

Herring gulls mostly lay three eggs (Graves *et al* 1984, Cramp and Simmons 1985), with a surprisingly small number laying more or less than three. Clutches of four are extremely uncommon, and are often interpreted as being the product of female-female pairings (e.g. Spaans *et al* 1987). In previous studies, pairs laying clutches of one or two eggs were found to breed less successfully than birds laying three eggs, suffering lower hatching success per egg as a result of high egg predation (Paynter 1949), and lower fledging success per egg (Hébert and Barclay 1988). These studies made no attempt to distinguish

between genuine clutches of one or two, and clutches that were partially predated during egg-laying or shortly thereafter. If the adults with partially predated clutches were on average lower 'quality' than non-predated pairs, then the inclusion of these in the one and two egg categories would increase the overall 'quality' of the three egg category and reduce that of the one and two egg categories. This could potentially produce the differences in breeding success between the apparent clutch sizes (Harris 1964).

Egg size

Breeding gulls can manipulate their total investment in a clutch (total clutch volume) and the way in which this parental investment is allocated to each potential offspring through the way in which they apportion energy or nutrients to their clutch (through both absolute egg size and the ratio of volumes of individual eggs to each other. Hébert and Barclay 1988).

Egg volume has been shown to correlate with hatching weight, hatching size, growth rate, chick survival and fledging weight (e.g. Parsons 1970. See Perrins and Birkhead 1986 fora full list of examples). These findings have led several authors to suggest that selection should favour increased egg size (e.g Parsons 1975, Bolton 1991); however no attempt has been made to identify the counter-balancing selection pressure that prevents an increase in egg size, such as increased production costs.

The aim of this part of the study was to investigate the way in which breeding gulls organise their pattern of reproductive investment at the egg production stage, and the way that this affects breeding success. From these results, it was hoped to discover ways in which Herring Gulls manipulate there reproductive investment such as to maximise breeding output from an individual breeding bout.

METHODS

General methods are described in chapter 2. The bulk of this investigation was carried out on Sanda; however data on clutch size, individual egg volumes and clutch volumes were collected at Walney as part of other investigations and are also presented in this chapter. The methods used in this part of the study differ from those described in Chapter 2 in the following ways;

Laying date

Due to the small proportion of clutches that comprised of less than three eggs, clutch size data from each colony were grouped into four periods to ensure sufficient numbers of smaller clutches in each period to allow statistical analysis. At both colonies, median laying date and quartiles were used to split laying into four periods (see table 5.1 for actual values)

Clutch size

As nests were visited normally on alternate days and eggs marked, predation of eggs that had been in the nest on average >36 hours could be detected. After predation of an egg has taken place, some shell or other remains could often be found; these were searched for when an expected egg had not appeared. To prevent misrecording of three-egg clutches predated immediately after the *c* egg was laid and before the nest total clutch had been recorded, clutch size was only classified as "definite" if the nest contents remained for more than three days (the *c* egg is on average laid 49.1 hours later (Parsons 1976)). 1-egg clutches were found at both Sanda and Walney. None of these were found to hatch and when the 1-egg clutches on Sanda were visited during "incubation", all were found to be cold on all visits, and on no occasion was an adult seen incubating. For this reason, and following Harris (1964), these clutches were assumed to be nesting efforts that had been abandoned during laying and not included in analyses of clutch size.

RESULTS

Laying date effects

Clutch size

Clutch size was not found to decline with laying date at either Sanda (Table 4.1) or Walney (Tables 4.2). At Walney, there was no difference in the proportion of C3's recorded in the first two and second two periods (due to the small number of clutches smaller than 3, analysis by period was not possible). Analysis of the Sanda data revealed no difference in the proportion of C3's in each period (X^2=3.458, 3 d.f., N.S.), or between the first half and second half of the laying period (X^2 with Yates' correction factor = 1.674, 1 d.f., P>0.05). Laying date showed no relationship with clutch size.

Egg volumes

There was no relationship between laying date and the volumes of *a* and *b* eggs from C3's at either colony. On Sanda the *c* egg and the total clutch volume for C3's were also unrelated (Table 4.3); however on Walney these showed a significant decline through the season (Table 4.4). Egg volumes for C2's also showed no relationship with laying date (Table 4.3).

Breeding success

A decline in the mean number of chicks hatching from C3's was recorded; however this was not statistically significant (Table 4.5). The number of chicks successfully fledged from C3's did not vary between laying periods (Table 4.5).

Clutch size effects

Egg volume within each clutch size

On Sanda, *a* and *b* eggs did not differ in volume in C3's, but were both larger than *c* eggs (Table 4.6). At Walney this trend was repeated, but the difference in size between the *a*

Table 4.1 - Clutch size with laying period, Sanda 1989

	Laying Period				
Clutch	1	2	3	4	Total
3	36	42	37	31	146
2	6	8	6	15	35
Total	42	50	43	46	181
Mean	2.86	2.84	2.86	2.67	2.69

Kruskal-Wallis 1-way ANOVA corrected for ties, H=6.86, P=0.076.
Proportion of 2 and 3-egg clutches in each period X^2=7.01, 3 d.f., P>0.05.

Table 4.2 - Clutch size with laying period, Walney 1990

	Laying Period				
Clutch	1	2	3	4	Total
3	36	43	27	39	144
2	3	1	3	4	11
Total	40	46	30	45	161
Mean	2.88	2.89	2.93	2.82	2.86

Kruskal-Wallis 1-way ANOVA corrected for ties, H=3.01, N.S.
Proportion of 2 and 3-egg clutches in each period X^2=0.77, 3 d.f., N.S.

Table 4.3 - Effect of Laying date on total clutch volume (T.C.V.) and the volume of eggs by laying order, for 2 and 3-egg clutches/Sanda 1989.

CLUTCH SIZE	EGG	n	r	r^2	b	S_b	A	P
3	A	90	0.10	0.01	0.11	0.12	75.3	0.35
	B	79	-0.12	0.02	-0.19	0.17	78.4	0.28
	C	97	0.02	0.00	0.03	0.12	70.4	0.82
	T.C.V.	122	-0.02	0.00	-0.06	0.28	225.3	0.82
2	A	25	-0.10	0.01	-0.09	0.20	75.2	0.65
	B	25	-0.31	0.09	-0.28	0.18	76.2	0.12
	T.C.V.	29	-0.26	0.07	-0.51	0.37	156.5	0.18

Where n= sample size
r= correlation coefficient
b= slope
S_b= standard error of slope
A= intercept
P= significance

able 4.4 - Effect of Laying date on total clutch volume (T.C.V.) and the olume of eggs by laying order, for 3-egg clutches/Walney 1990.

EGG	n	r	r^2	b	S_b	A	P
A	62	-0.01	0.00	-0.02	0.19	79.7	0.91
B	49	-0.15	0.02	-0.18	-0.17	79.8	0.30
C	52	-0.40	0.16	-0.49	0.16	76.0	0.003
T.C.V.	65	-0.37	0.14	-1.35	0.43	240.2	0.003

Where n= sample size
r= correlation coefficient
b= slope
S_b= standard error of slope
A= intercept
P= significance

Table 4.5 - Hatching and fledging success of clutches of three eggs split by laying period, Sanda 1989.

	LAYING PERIOD 1	2	3	4	Mean
Number of clutches	36	42	37	31	-
Mean number hatched per clutch	2.69	2.43	2.35	1.94	2.35
Mean number of chicks fledged per clutch	0.89	0.95	0.87	0.55	0.84

Hatching Success - Kruskal Wallis 1-way ANOVA, H=5.21, N.S.
Fledging Success - Kruskal Wallis 1-way ANOVA, H=3.83, N.S.

Table 4.6 - Paired t-tests of egg volumes (cm^3) by laying order, within clutches, split by colony and clutch size.

COLONY	C[1]	EGG	n=	Mean	s.d.	EGG	n=	Mean	s.d	t*	P
WALNEY 1990	3	A	47	80.02	6.74	B	47	78.69	5.86	1.92	0.062
		B	45	79.06	5.62	C	45	72.54	5.55	10.49	0.000
		A	44	80.32	6.64	C	44	72.66	5.55	8.60	0.000
	2	A	3	71.99	5.20	B	3	67.80	0.45	1.29	0.327
SANDA 1989	3	A	85	77.15	6.49	B	85	76.27	7.63	1.32	0.191
		B	82	76.27	7.75	C	82	70.55	5.44	7.97	0.000
		A	82	77.24	6.38	C	82	70.54	5.45	10.83	0.000
	2	A	25	73.77	6.81	B	25	71.00	5.64	2.16	0.044

[1] Column C represents clutch size.

* Results of Student's t-test between eggs in each row of the table i.e. comparisons of egg volume between different eggs in the laying sequence within a clutch.

egg and the *b* egg approached significance (Table 4.6). On Sanda the *b* eggs from C2's were smaller than *a* eggs from C2's (Table 4.6)

Comparison of egg volumes between clutch sizes

Comparisons between egg volumes for eggs from C2's and C3's were only possible using the data for Sanda (see table 4.6 for values), as the sample sizes for Walney were too small. On Sanda *a* eggs from C3's were larger than from C2's (T=-2.55, df 120, P=0.012 Table 4.6). The same was true for *b* eggs (T=-2.93, df 109, P=0.004 Table 4.6). The *a* egg from C2's did not differ from the *b* egg from C3's (T=-1.54, P=0.125 Table 4.6), and the *b* egg from C2's did not differ from the *c* egg from C3's (T=0.37, P=0.713 Table 4.6). See Figure 4.1 for summary.

Breeding success

Hatching success was lower for individual eggs from C2's than C3's (Table 4.8). The proportion of hatched chicks that survived to fledging was higher for chicks from C3's than C2's (Table 4.8). The proportion of eggs that produced fledged young was higher from C3's than for C2's (Table 4.8).

Effect of egg size on breeding success

The mean volumes of eggs that hatched and eggs that failed to hatch were not different for any egg in the laying sequence, in C2's or C3's (Table 4.9). The mean volumes of eggs that did hatch and subsequently produced fledged chicks was not different from those that hatched and failed to fledge chicks (Table 4.10). As with hatching success, this was true of all eggs in the laying order, for both C2's and C3's. Combining hatching and fledging success, the mean volumes of eggs that produced fledged young was not different from those that failed to do so (either through failing to hatch or the chick dying), for any egg in C2's or C3's (Table 4.11). Egg volume therefore had no detectable effect on breeding success.

Table 4.7 - Hatching and fledging success of clutches of 2 and 3 egg clutches, Sanda 1989

	CLUTCH SIZE 2	3
Number of clutches	35	146
Mean number hatched per clutch	0.97 (0.99)	2.35 (1.23)
Mean number of chicks fledged per clutch	0.17 (0.38)	0.84 (0.95)

N.B. Brackets indicate standard deviation

Table 4.8 - Success of individual eggs from 2 and 3-egg clutches/ Sanda 1989

	Clutch Size 2	3
Number of Eggs (E)	70	441
Number Hatching (H)	50	378
Number Failed	20	63
% Hatching	71.4	85.7
Number Fledging (F)	6	123
% Chicks Fledged (F/Hx100)	12.0	32.5
% Eggs producing Fledged young (F/Ex100)	8.6	27.9

Proportion of eggs hatching in each category - X^2 with Yates' correction = 7.97, 1 d.f., $P<0.005$.
Proportion of eggs that hatched that subsequently fledged young - X^2 with Yate's correction = 7.95, 1 d.f., $P<0.005$.
Proportion of eggs that fledged young - X^2 with Yates' correction = 10.99, 1 d.f., $P<0.001$

Table 4.9 - Comparison of egg volumes for eggs that hatched and those that failed to hatch from 3-egg clutches, Sanda 1989.

Clutch Size	Egg	Hatched n=	Hatched Mean	Hatched s.d.	Failed n=	Failed Mean	Failed s.d.	t*	df	P
3	A	84	77.12	6.29	12	77.84	5.38	0.38	94	0.708
	B	76	76.00	7.57	10	77.95	8.01	0.76	84	0.448
	C	93	71.18	5.57	10	68.35	7.05	-1.49	101	0.140
2	A	17	74.28	7.53	8	72.25	3.94	-0.71	23	0.484
	B	17	72.85	5.81	8	68.25	5.26	-1.90	23	0.070

* Result of Student's t-test

Table 4.10 - Comparison of egg volumes for eggs from 3-egg clutches that fledged young and those that hatched but failed to fledge young, Sanda 1989

Clutch Size	Egg	Fledged n=	Fledged Mean	Fledged s.d.	Failed n=	Failed Mean	Failed s.d.	t*	df	P
3	A	26	77.35	7.55	59	77.02	5.73	0.22	83	0.829
	B	31	76.66	6.72	45	75.54	8.14	0.64	74	0.527
	C	32	70.30	6.11	61	71.64	5.26	-1.10	91	0.274
2	A	4	74.52	12.82	13	74.21	5.88	0.05	12	0.965
	B	16	72.93	5.99	1	71.50	0.00	-0.23	15	0.820

* Result of Student's t-test

Table 4.11 - Comparison of egg volumes for eggs that produced fledged young and eggs that failed to produce fledged young, Sanda 1989.

Clutch Size	Egg	Fledged n=	Fledged Mean	Fledged s.d.	Failed n=	Failed Mean	Failed s.d.	t*	df	P
3	A	26	77.35	7.55	71	77.16	5.64	-0.13	95	0.897
	B	31	76.66	6.72	55	75.97	8.10	-0.40	84	0.689
	C	32	70.30	6.11	71	71.17	5.60	0.71	101	0.478
2	A	13	74.34	7.61	12	72.86	5.48	-0.55	23	0.586
	B	1	71.50	0.00	24	71.37	6.07	-0.02	23	0.984

* Result of Student's t-test

SUMMARY OF RESULTS

Neither laying date nor egg volume had any detectable effect on breeding success on either Sanda or Walney. The only effect of laying date was on the volume of the *c* egg and total clutch volume on Walney, which both declined as the season progressed. Clutch size at Walney and Sanda, *a* and *b* egg volumes at both colonies, total clutch volume and *c* egg volume at Sanda, number of eggs hatched per clutch and number of chicks fledged per brood, were all unaffected by laying date. Egg volumes had no effect on hatching, fledging or overall breeding success.

In contrast, clutch size showed a positive relationship with hatching and fledging success per egg. This result was found with more accurately identified clutches of two and three (see methods), showing that previous findings were not simply due to misidentification of partly predated clutches.

DISCUSSION

The lack of any relationship between laying date and breeding parameters, and between egg volume and breeding parameters is contrary to the findings of many similar investigations on Herring Gulls (Parsons 1972), however other studies have similarly found no relationships between laying date and breeding parameters (e.g. Davis 1975). This apparent contradiction, may be the result of different levels of breeding success at the colonies studied. Several studies have been carried out at individual colonies in years of high and low breeding success (Table 4.12). If one looks at the differences in detected trends between seasons, then one finds that in years of lower breeding success, several factors affect breeding success that do not in better breeding seasons. For example, Davis (1975) found that on Skokholm in a year of low breeding success (0.60 chicks fledged per pair), a seasonal decline in hatching success occurred. In a year of higher breeding success (0.70 chicks fledged per pair), this trend was not observed. In all of the other studies, relationships were found in years of low breeding success, that were not found in better

Table 4.12 - Gull studies in which inter-seasonal differences in breeding success have coincided with differences in other findings.

SPECIES	AUTHOR	GOOD YEAR	BAD YEAR	MEASURE OF SUCCESS	FINDINGS MADE IN ONE SEASON ONLY
Herring gull	Davis (1975)	1972	1970	Fledging	1970 - seasonal decline in hatching success. Positive correlation between hatching weight and fledging success per chick. 1972 - None.
Herring gull	Parsons et al (1976)	1966 1967	1968	Subsequent recruitment of cohorts to colony	1968 - Post-fledging survival negatively related to hatch date. 1966 - None. 1967 - None.
Herring gull	Pierotti (1982)	1978	1977	Fledging	1978 - More differences in chick growth rates and egg volumes between habitats than in 1977. 1977 - None.
Glaucous-winged gull	Murphy et al (1984)	1979	1980	Fledging	1980 - Fledging success negatively related to hatch date. 1979 - None.
Glaucous-winged gull	Hunt + Hunt (1976)	1973	1971	Fledging	1971 - Territory size and growth rates positively related to chick survival Hatch date negatively related to chick survival. Adults left chicks unguarded longer at the end of the season 1973 - Growth rate positively related to chick survival at the very end of the season.

breeding seasons. In no case was the reverse true, with relationships being found in years of high breeding success but not in years of low breeding success. Sanda and Walney both enjoyed higher levels of fledging success than the studies in Table 4.12, (0.84 and 0.88 chicks fledged per pair respectively, see chapter 6 for a discussion of levels of breeding success found in other studies).

To understand why differences in these relationships occur between years of different breeding success, one must first establish the ways in which egg volume and laying date can affect breeding success.

Egg size effects

Egg volume has been shown to positively affect breeding success in many ways (see introduction). This effect has recently been demonstrated to be partly due to the effects of egg volume directly, and partly due to the fact that birds laying larger eggs are "higher quality" (in terms of foraging ability and parental abilities) birds than those laying small eggs (Bolton 1991). Increased egg size was found to result in skeletally larger, proportionally heavier chicks than those from small eggs (Bolton 1991). Part of the reason for this increased weight is the presence of larger reserves, which may be important in helping the chick survive the first few days post-hatch (Parsons 1970). In years of high food availability, this extra provisioning of yolk may have a negligible effect on chick survival, as parents would presumably have little difficulty in finding food.

Laying date effects

Investigations into the effect of laying date on breeding success suffer from the same kind of confounding factors as the study of egg volume, with young inexperienced birds and lower "quality" birds breeding later in the season than older birds (Parsons 1972, Mills 1975). Parental quality and age effects have not yet been experimentally manipulated in such a way as to establish whether laying date *per se* affects breeding success.

It is difficult to see how laying date could have a great influence in a species that breeds so synchronously as the Herring gull. Timing of breeding means that peak chick energy demand (3-4 weeks post-hatch (Dunn 1976)) coincides with the annual maximum number of hours of daylight, allowing adults gulls to forage longer per day than at other times of the year. The number of daylight hours however varies very little two weeks either side of midsummer so it is unlikely that time available for foraging could produce the observed trends in breeding success. The presence of important food types varies little during the chick rearing period, important items being available from long before until long after the chick-rearing period (Pierotti and Annett 1986). Whilst this may suggest that food availability is not limiting, these prey sources may become depleted by early breeders. As a result, early breeders would in effect be competition-free whereas later breeders would be foraging for prey already depleted. Differences in the availability of food around a Herring Gull colony as the breeding season progresses has not been assessed so this hypothesis cannot be tested.

Laying date has been shown to affect post-fledging survival (Parsons *et al* 1976). This could be due to parental quality effects again, but it would also seem likely that chicks fledged earlier in the season will have longer to develop/learn foraging skills necessary to survive food shortages post-fledging. Herring gulls show considerable age-related differences in foraging ability, implying that foraging skills do take a long time to acquire (Greig *et al* 1983). Herring Gull fledglings are fed on territory by their parents for at least four weeks (Cramp and Simmons 1983), and continue to beg to adults even into their second winter. It is not however known when a reduction in food provided by adults results in fledglings having to be able to feed themselves to survive. Adult Herring Gulls are at their lowest body weight at the end of summer (Coulson *et al.* 1983b) suggesting that this is a time of low food availability, however to what extent this low body weight is a result of the breeding effort is not known. Kadlec and Drury (1968) considered first winter to be the crucial time in fledgling survival.

Clutch size effects.

If clutch size is optimised to produce a brood that will result in the parents working at their "optimal work load", then within a colony it is reasonable to assume that birds laying smaller clutches are lower "quality" birds than birds laying larger clutches. In this study, birds laying C2's bred less successfully than birds laying C3's, both in terms of hatching and fledging success. The negative effect that inclusion of partly predated clutches would have on the C2 category's breeding success (see methods) was largely removed in this study by more accurate recording of clutch size than in previous studies. These results show that birds that lay two eggs are less successful at both the egg and chick stage of the breeding cycle than birds that lay three eggs and that this is not a result of mis-classification of clutch sizes.

Comparisons of egg volume between eggs from C2's and C3's, show that rather than C2's comprising the equivalent to *a* and *b* eggs from a C3, they more closely resemble the *b* and *c*. This supports the findings of Hébert and Barclay (1988). They offered no explanation for this observation. However it is clear that the presence of a smaller egg at the end of the laying sequence is true not only of C3's, but also of C2's.

The presence of a smaller *c* egg in clutches of three has been explained as being due to laying females 'running-out' of reserves available at the end of clutch formation (Nisbet 1973, Houston *et al* 1983)). Hypothesised reserves that have been implicated have included energy (Nisbet 1973, Houston *et al.* 1983), sulphur amino acids (Houston *et al.* 1983), calcium (Pierotti and Annett 1986) and manganese (Pierotti and Annett 1986). If this was true, then the size of the *c* egg should vary between females, reflecting the level of reserves each female has available for the formation of the last egg. Consequently, one would expect the *c* egg to vary in size from full *a* egg size to the smallest minimal viable egg size. This would be reflected in a high variance of *c* egg volume; however this is not the case (Coefficients of Variation - Sanda *a* egg=8.41, *b* egg=10.00, *c* egg=7.71, Walney *a* egg=8.42, *b* egg=7.45 and *c* egg=7.64). Re-stating the hypothesis, it is possible that

females have an upper limit to the amount of reserves they can store and that this results in there not being enough of a particular reserve for the female to produce a full-sized last egg. The presence of a smaller last laid egg in clutches of two refutes this. Females laying a clutch of two would not be affected by this upper limit to reserves and should thus vary in the level of reserves available for the formation of the last egg. However, as with the *c* eggs, *b* eggs from C2's do not show higher variability than either the *a* egg, or from the eggs in a C3. (Coefficient of Variation for eggs from 2-egg clutches - Sanda = *a* egg=9.23 *b* egg =7.94, Walney *a* egg=7.22, *b* egg=6.64. See also Hèbert and Barclay 1988)

Another possible explanation for the smaller size of the last-laid egg, is that as clutch completion approaches, the females' follicles degenerate and consequently a smaller egg is laid (Parsons 1976). Parsons (1976) induced laying females to lay more than three eggs by removing eggs as they were laid. He found that, in nests where the *a* egg was removed immediately after laying, three more eggs would be laid. These eggs resembled a normal clutch, with the last laid (the "*d*" egg) being significantly smaller than the two other eggs. If however the *a* egg was left in the nest, and the *b* egg removed, then only the *c* egg would be laid. This was smaller than the other two eggs, and was the size of a normal *c*. Parsons interpreted these results as indicating that the stimulus of the *a* egg causes the follicles of the laying female to reduce in size resulting in a smaller last laid egg. The switch in behaviours from egg-laying to incubating has been demonstrated to involve the secretion of prolactin which in turn suppresses the secretion of gonad-stimulating hormones (Romanoff and Romanoff 1949). If, as Parsons argued, the presence of the *a* egg caused the female to switch behaviour from egg-laying to incubating, and this in turn caused the last-laid egg to be smaller, then follicle degeneration must not take effect until after the *b* egg is laid. The *b* egg is normally the same size as the *a* egg (e.g. Harris 1964). If this was true, then birds laying two egg clutches would not have an *a* egg in the nest long enough for follicle degeneration to affect the last laid egg. This assumes that the laying span for a C2 is not the same as for a C3 (over 4 days between the laying of the first and last egg). This has not been studied, however it would seem a reasonable assumption. Any

reduction in the size of the second egg in a C2 is therefore unlikely to be the result of follicle degeneration. Unless follicle degeneration occurs at a different rate in birds laying two egg clutches, or C2's take as long to lay as C3's, then this hypothesis explaining the small size of last-laid eggs can be rejected.

None of the contempary hypotheses explaining the small size of the *c* egg in C3's can explain why a smaller last laid egg is also found in clutches of 2. A discussion of the adaptive nature of the small size of the last laid egg in the Herring Gull forms part of the basis for the discussion Chapter 7.

The effects of modifying reproductive investment at the egg production stage

Breeding Herring gulls can alter their breeding effort at the egg production stage either by increasing egg volume, laying earlier, or increasing their clutch size. The latter does seem to occur with clutch sizes increasing in good breeding seasons (e.g. Hunt and Hunt (1975), Becker and Erdelen (1986)), with the proportion of C3's increasing. However, even in excellent years C4's are extremely rare. Herring gulls appear to be constrained to laying a clutch of three eggs; most breeding birds cannot therefore increase their reproductive output through increasing clutch size. Hiom *et. al.* (1991), provided supplementary food to Lesser Black-backed gulls in the pre-laying period and found that in years of high food availability, supplemetary-fed females did not produce larger clutches than did control females. In a year of very poor food availability, the extra food allowed experimental birds to lay 3-egg clutches while more of the un-fed control birds laid 2-egg clutches. These results suggest that clutch size is increased by the provision of extra food, but only to a maximum of 3 eggs.

Egg volume affects breeding success in poor breeding seasons (e.g. Davis 1975); however, in good seasons it has no detectable effect (e.g. this study). In years of high food availability, when parents have extra resources to invest in a breeding bout, increasing egg

size will have no effect.

The remaining aspect that breeding birds can control is their laying date, however laying date has no effect on breeding success in years of high breeding success (e.g. Davis 1975, Parsons *et al* 1976, this study). In colonially nesting birds such as the Herring Gull, early nesters are also penalised as a result of increased con-specific predation of eggs and chicks (Brown 1967). Breeding Herring Gulls cannot improve their breeding success by breeding earlier than other birds in the colony.

In years of high food availability, breeding Herring gulls do not seem able to alter their pattern of reproductive organisation in any way that will increase breeding success other than to lay earlier (and this will only be successful if the colony peak laying date becomes earlier). Egg volume has little effect on survival, and in all but a very few cases, clutch size is limited to three. The constraint on laying date is not unexpected for a colonially nesting bird, and has been documented in several other species (see Gochfield 1980). The constraints on clutch size, egg volume and the size of the last laid egg however, run contrary to conventional theories regarding reproductive investment in birds. These apparent contradictions form the basis of Chapter 7.

CHAPTER 5

FACTORS AFFECTING BREEDING SUCCESS WITHIN COLONIES: DIFFERENCES BETWEEN SAMPLE PLOTS AND EFFECTS OF PHYSICAL CHARACTERS OF NEST SITE

INTRODUCTION

The study of breeding success in species of seabirds that breed in large colonies requires the sampling of sub-populations within those colonies, and subsequent extrapolation of the results to the population level. In the Herring gull, many studies involve monitoring of only one sample plot (e.g. Paynter 1949), or fail to incorporate a measure of intra-colony variation in breeding success when extrapolating to population level (e.g. Harris 1964). The validity of extrapolating results from sample plots to the population level has not been investigated in gulls, in spite of several investigations demonstrating variation in breeding parameters between different areas of a colony (e.g. Becker and Erdelen 1986). At a colony such as Sanda, with a rapidly increasing Herring gull population, it is particularly important to choose sample plots carefully, as newly colonised areas are likely to be made up of young breeders. Young inexperienced birds differ from older breeders in laying date, clutch size, egg size and nest density, all of which can have profound influences on breeding success (see chapter 4).

To investigate any differences between sample plots, it was important to establish whether differences occurred in nesting habitat. Within colonies, nesting habitat has been shown to affect; nest density, laying date, clutch size, egg predation, hatching success, chick growth rates, chick predation, and fledging success (Brown 1967, Becker and Erdelen 1986, Pierotti 1982). Nest spacing also has an effect on breeding parameters including; egg size, chick survival and fledging success per brood (Hunt and Hunt 1976, Parsons 1976, Burger 1984, Kilpi 1989). To investigate whether differences between sample plots could be a result of differences in nesting habitat and density, these were recorded for each colony to see if they were consistent between sample plots. The breeding success of all nests was then analysed to establish whether either of these factors had an effect on any particular stage of breeding that could potentially explain differences between sample plots.

METHODS

Breeding parameters between sample plots

On Sanda, the breeding areas are well dispersed and form discrete sample plots (Figure 5.1); eight sample plots were chosen, five of which were discrete sample plots isolated from other breeding gulls, and three sample plots within the same large colony (numbers 5, 6 and 8). The methods used to monitor and record the breeding variables are as described in chapter 2. For analysis of egg volume, hatching success and chick survival, only data from nests that contained three eggs are used. Comparisons using smaller clutch sizes are not possible due to the small number of these found in each colony. Egg volume is calculated using the formula length x breadth^2 x 0.00476 (Harris 1964).

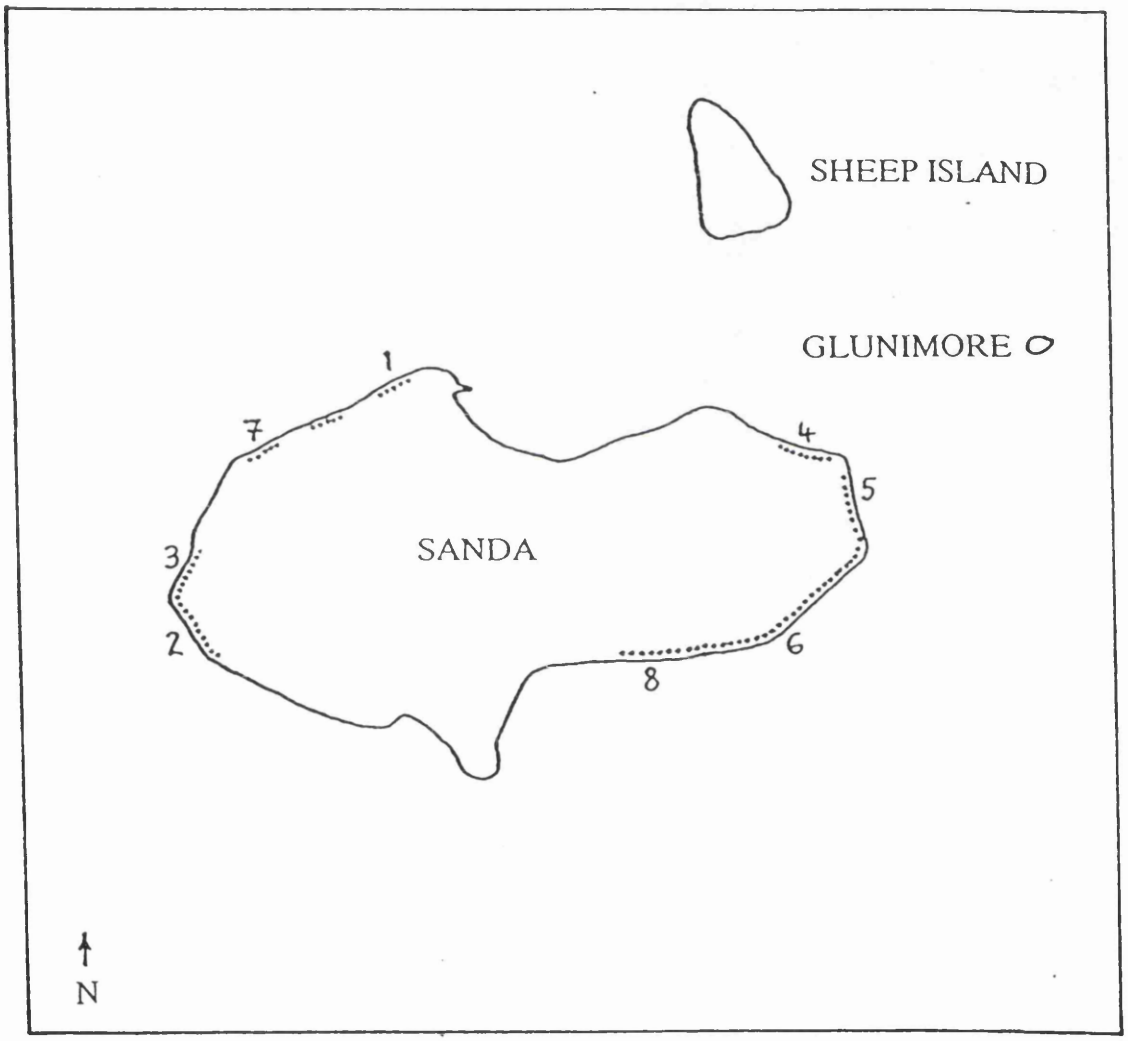
Nest density

The positions of all nests in three colonies (2, 3 and 8) were mapped. These were recorded by choosing an approximately central point in each sample plot and then measuring the distance of each nest from this point as well as the compass bearing form the central point to each nest. This allowed me to plot each colony on graph paper at a later date, from which I could then measure the number of nests within 5 metres of each nest, as a measure of density.

Nest cover

Each nest site was scored for nest cover. Nests were scored on four sides for cover that would effectively shelter an incubating/brooding adult sitting on the nest. This was taken as being cover greater than 30cm high within 0.5m of the nest site. The sides were scored clockwise, side one being the side nearest to the sea. Total nest cover was calculated by adding up the number of sides for which cover was recorded, so five categories of cover were possible (0-4).

Figure 5.1 The Sanda group of islands, showing the distribution of nesting Herring gulls (dotted areas)and study plots on Sanda.



Scale: 1 inch = 0.5 miles

Chick cover

Each nest site was scored for potential cover for chicks within 5m of the nest site or half way to a neighbouring nest if this was <10 metres away. Three categories were recorded; no cover (0), at least one site that could provide cover for a brood of three chicks less than 10 days old (1), at least one site that could shelter three chicks large enough to fledge (2).

Nest density, nest cover and chick cover were all recorded at the end of the breeding season to avoid disturbance of nesting gulls. By this time several nests markers had either disappeared or were no longer legible; for this reason sample sizes may not match those in other analyses. The measurement of chick cover at the end of the breeding season is likely to have exaggerated the amount of cover available as vegetation surrounding nests continued to grow throughout the breeding season. However, this is unlikely to have influenced the results, as plants growing in the colonies were mostly large enough to provide cover for small chicks at the time of hatching and grew rapidly thereafter, providing plenty of cover for older chicks. Vegetation provided no nest cover for any of the nests so the growth of vegetation will have had no effect.

RESULTS

Differences between sample plots in breeding parameters

Average laying date was found to differ significantly between sample plots (Table 5.1). Comparing between sample plots (following Siegel and Castellan 1988 pg 213, "mutiple comparisons between groups"), showed that this difference was not due to any particular sample plot, but to many differences e.g. sample plots 4 and 6. Average clutch size was not significantly different between sub-colonies/sample plots (Table 5.2).

Due to the small number of two egg clutches in each sample plot (Table 5.2), analysis of egg volume was only carried out on 3-egg clutches. The volumes of "a", "b" and "c" eggs did not vary between sample plots (Tables 5.3 to 5.5 respectively); however total clutch volume for 3-egg clutches did (Table 5.6). Using a Tukey range test (In SPSSX), to locate

Table 5.1 - Mean laying dates (measured as number of days after 24/4/89) for each sample plot on Sanda 1989.

Colony	n	Mean	sd	Median
1	25	17.32	7.19	16
2	25	20.80	9.37	18
3	19	19.26	6.26	20
4	31	17.42	6.09	16
5	19	14.11	7.49	14
6	23	11.65	6.02	10
7	22	15.77	8.41	14
8	23	14.35	5.90	12
All	187	16.43	7.56	16

Kruskal-Wallis 1-way ANOVA corrected for ties, $H=27.51$, $P<0.001$.

Table 5.2 - Distribution of clutch sizes between sample plots, Sanda 1989.

Colony	n	Clutch Size 2 (%)	3 (%)	Mean	sd
1	26	4 (15.4)	22 (84.6)	2.85	0.37
2	23	6 (26.1)	17 (73.9)	2.74	0.45
3	18	3 (16.7)	15 (83.3)	2.83	0.38
4	30	3 (10.0)	27 (90.0)	2.90	0.31
5	19	6 (31.6)	13 (68.4)	2.68	0.48
6	25	6 (24.0)	17 (68.0)	2.60	0.65
7	21	4 (19.0)	17 (81.0)	2.81	0.40
8	24	3 (12.5)	19 (79.2)	2.71	0.62
All	186	35 (18.8)	146 (78.5)	2.77	0.47

Proportion of nests with 2 or 3 eggs not different between sample plots ($X^2=5.58$, 7 d.f., N.S.)

Table 5.3 - Volumes of "a" eggs from 3-egg clutches, for each colony, Sanda 1989.

Colony	n=	Mean (ml)	sd
1	15	77.83	4.91
2	10	76.57	8.11
3	9	77.83	3.92
4	18	76.08	4.29
5	12	81.13	5.52
6	10	74.90	10.41
7	12	75.61	4.49
8	11	77.88	6.65
All	97	77.21	6.17

ANOVA $F_{7,89}=1.177$, N.S.

Table 5.4 - Volumes of "b" eggs from 3-egg clutches, for each colony Sanda/1989

Colony	n=	Mean (ml)	sd
1	14	77.16	4.54
2	9	77.05	6.81
3	8	71.90	15.64
4	15	74.00	6.64
5	11	80.50	6.98
6	9	75.76	8.96
7	10	76.10	4.51
8	10	76.80	4.43
All	86	76.22	7.60

ANOVA $F_{7,78}=1.121$, N.S.

Table 5.5 - Volumes of "c" eggs from 3-egg clutches, for each colony Sanda/1989.

Colony	n=	Mean (ml)	sd
1	16	72.82	5.51
2	11	69.42	6.39
3	10	69.18	3.32
4	18	69.34	7.25
5	11	73.78	5.06
6	10	70.30	6.39
7	14	69.96	4.23
8	13	72.34	5.54
All	103	70.90	5.75

ANOVA $F_{7,95}=1.280$, N.S.

Table 5.6 - Total clutch volumes of three egg clutches from each colony/Sanda 1989.

Colony	n=	Mean	sd
1	18	231.31	17.51
2	13	222.53	19.43
3	12	217.99	15.62
4	26	221.01	14.59
5	13	237.15	14.39
6	16	223.80	21.58
7	17	222.36	12.74
8	16	228.06	16.91
All	131	225.28	16.91

ANOVA $F_{7,123}=2.119$, $P<0.05$

differences between groups revealed that they occurred between sample plot 5, and both sample plot 3 and 4.

Hatching success per clutch differed between colonies (Table 5.7). Due to the small number of eggs failing to hatch, comparisons within the laying sequence were not possible. The proportion of eggs "disappearing" from each colony was different (X^2=20.7, 7 d.f., P<0.05. Table 5.8).

The number of chicks fledged per clutch differed between sample plots (Table 5.7). This was not due solely to the difference in hatching success between sample plots as the proportion of chicks that hatched and subsequently fledged also differed between sample plots (X^2=14.183, 7 d.f., P<0.05. Table 5.8).

Differences between sample plots in territory size/quality.

The density of nests between the three sample plots were different (Table 5.9). Multiple comparisons between groups (following Siegel and Castellan 1988), revealed that this was due to differences between all 3 groups. The proportion of nests in each sample plot with 50% nest cover (at least two sides) was different (Table 5.10). The proportion of nests in each sample plot that contained no chick cover also differed between sample plots (X^2=47.37, 7.d.f., P<0.01. Table 5.11). Due to the small number of nests with cover scores of 2, it was not possible to analyse this by sample plot. However the data show that the proportion of nests with a cover score of 2 varied widely between sample plots, from 77.8% (plot 6) to 0% (plot 4).

Effects of territory size/quality on breeding parameters.

Effect of nest density on breeding parameters

Nest density had no effect on either hatching success for clutches of three (Table 5.12) or on fledging success from broods of three (Table 5.13).

Table 5.7 - Comparison of mean hatching/fledging success of three-egg clutches for each sample plot, Sanda 1989.

	SUB-COLONY								
	1	2	3	4	5	6	7	8	Mean
Number of clutches	22	17	15	27	13	17	17	19	-
Mean number hatched per clutch	2.32	2.29	1.60	2.19	2.08	2.94	2.29	3.00	2.35
Total number of chicks hatched	51	39	24	59	27	50	39	57	-
Total number of chicks fledged	23	9	12	15	11	24	11	18	-
% of hatched chicks that fledged	45.1	23.1	50.0	25.4	40.7	48.0	28.2	31.6	-
Mean number of chicks fledged per clutch	1.05	0.53	0.80	0.56	0.85	1.41	0.65	0.95	0.84

Hatching success per clutch - Kruskal-Wallis 1-way ANOVA corrected for ties, $H=15.08$, $P<0.05$.
Fledging success per clutch - Kruskal-Wallis 1-way ANOVA corrected for ties, $H=13.86$, $P=0.05$.
Proportion of hatched chicks that survived to fledge - $X^2=14.18$, 7 d.f., $P<0.05$.

Table 5.8 - Individual egg results for eggs from 3-egg clutches, by sample plot/Sanda 1989

	SUB-COLONY								
	1	2	3	4	5	6	7	8	Total
Dissappeared	9	12	9	11	12	6	5	1	65
(%)	13.6	23.5	20.0	13.6	30.8	11.8	9.8	1.8	14.7
Failed to hatch	3	0	2	7	0	4	0	3	19
(%)	4.5	-	4.4	8.6	-	7.8		5.3	4.3
Hatched	38	37	18	50	24	41	36	43	287
(%)	57.6	72.5	40.0	61.7	61.5	80.4	70.6	75.4	65.1
Presumed	12	2	15	7	3	0	10	9	58
hatched (%)	18.2	3.9	33.3	8.6	7.7	-	19.6	15.8	13.2
Broken in	4	0	1	6	0	0	0	1	12
nest (%)	6.1		2.2	8.1	-	-	-	1.8	2.7
Totals	66	51	45	81	39	51	51	57	441

Proportion of eggs that dissappeared by sample plot, $X^2=20.7$, 7 d.f., $P<0.01$.

Table 5.9 Frequencies of neighbours within 5m of each nest by sample plot, Sanda 1989

Sub-colony	Nests within 5m 0	1	2	3	4	5+	n=	Mean
2	3	2	2	1	1	0	9	1.44
3	1	0	1	2	3	8	15	4.80
8	0	4	4	5	5	0	18	2.61

Kruskal-Wallis 1-way ANOVA corrected for ties H=15.36, P=0.0005

Table 5.10 - Number of nests with each nest cover score by sample plot

	1	2	3	4	5	6	7	8	Total
0	5	1	9	2	4	0	6	3	30
(%)	21.7	5.6	60.0	9.5	21.1	0.0	31.6	15.0	19.6
1	8	8	3	4	7	1	5	7	43
(%)	34.8	44.4	20.2	19.0	36.8	5.6	26.3	35.0	28.1
2	7	3	3	7	1	3	5	2	31
(%)	30.4	16.7	20.0	33.3	5.3	16.7	26.3	10.0	20.3
3	2	2	0	7	3	8	2	6	30
(%)	8.7	11.1	-	33.3	15.8	44.4	10.5	30.0	19.6
4	1	4	0	1	4	6	1	2	19
(%)	4.3	22.2	-	4.8	21.2	33.3	5.3	10.0	12.4
Mean	1.39	2.00	0.60	2.05	1.79	3.05	1.32	1.85	1.77
n	23	18	15	21	19	18	19	20	153
median	1	1.5	0	2	1	3	1	1.5	2

Proportion of nests with 50% of sides covered significantly different between sample plots - X^2=32.00, 7 d.f., P<0.01.

Table 5.11 - Chick cover scores for individual nests within each sample plot

Chick cover	Sub-colony 1	2	3	4	5	6	7	8	Total
0	8 (34.8)	6 (26.1)	3 (20.0)	18 (78.3)	9 (50.0)	0 (0.0)	0 (0.0)	9 (47.4)	53 (34.6)
1	14 (60.9)	10 (43.5)	11 (73.3)	5 (21.7)	2 (11.1)	4 (16.0)	13 (68.4)	8 (42.1)	67 (43.8)
2	1 (4.3)	2 (8.7)	1 (6.7)	0 (0.0)	7 (38.9)	14 (77.8)	6 (31.6)	2 (10.5)	33 (21.6)
Mean	0.70	0.78	0.87	0.22	0.89	1.78	1.32	0.63	0.87
n=	23	18	15	23	18	18	19	19	153
Median	1	1	1	0	0.5	2	1	1	1

Proportion of nests with no cover varied between colonies $X^2=47.37$, 7.d.f., $P<0.01$

Table 5.12 - Effect of nest density on hatching success

	Nests within 5m 0	1	2	3	4	5+	Total
Mean	2.80	3.00	2.57	2.63	2.00	2.25	2.49
Median	3	3	3	3	3	3	3
n	5	6	7	8	9	8	43

Kruskal-Wallis 1-way ANOVA corrected for ties, H=4.01, N.S. (densities 0-1, 2-3 and 4-8 combined for analysis)

Table 5.13 - Effect of nest density on chick survival

	Nests within 5m 0	1	2	3	4	5+	Total
Mean	0.00	0.33	0.67	0.57	0.50	0.50	0.44
Median	0	0	0.5	0	0.5	0	0
n	5	6	6	7	6	6	36

Kruskal-Wallis 1-way ANOVA corrected for ties, H=2.92, N.S. (categories 0-1, 2-3 and 4-8 combined for analysis)

Effect of cover around nest on breeding parameters

No difference was found in hatching success from clutches of three between nests with different degrees of nest cover (Table 5.14). There was also no difference in fledging success from broods of three (Table 5.15). Clutch size did however vary between nests with different amounts of nest cover (Table 5.16). Comparing between the categories in the Kruskal-Wallis ANOVA (following Siegel and Castellan 1988, pg 213), the only difference that was found was that birds with nests with some cover (score 1-4), laid larger clutches than did birds with nests with no cover.

Effect of suitable chick cover on breeding parameters

Chick cover had a marked effect on chick survival from broods of three (Table 5.17), with the increases in the amount cover available to a brood of 3 chicks <10 days old, and the amount of cover available to a brood of 3 chicks up to fledging both resulting in increased chick survival (differences were found between all groups, following Siegel and Castellan 1988, pg 213). Hatching success from clutches of three followed a similar trend, however this only approached significance (Table 5.18). Clutch size did not vary between nests with different degrees of chick cover (Table 5.19).

SUMMARY OF RESULTS

Large differences in breeding parameters were found between the eight sample plots on Sanda; median laying date (9 days), mean total clutch volume (9%), mean hatching success per clutch (1.4 chicks) and mean fledging success per pair (0.88 chicks). Differences in the physical environment of nests in each colony were found for all three variables recorded; nest density, nest cover and cover available for chicks around the nest site.

Table 5.14 - Hatching success of clutches of three, by nest cover.

	Total cover					
	0	1	2	3	4	Total
Mean	2.33	2.43	2.41	2.84	2.65	2.52
Median	3	3	3	3	3	3
n	18	37	27	25	17	124

Kruskal-Wallis 1-way ANOVA corrected for ties, H=2.89, N.S.

Table 5.15 - Number of chicks fledged from broods of three, by nest cover.

	Total cover					
	0	1	2	3	4	Total
Mean	0.64	0.30	0.57	0.50	1.00	0.55
Median	0	0	0	0	1	0
n	14	30	21	24	15	104

Kruskal-Wallis 1-way ANOVA corrected for ties, H=6.6, N.S.

Table 5.16 - Mean clutch size against nest cover

	Total cover					
	0	1	2	3	4	Total
Mean	2.60	2.86	2.90	2.83	2.89	2.82
Median	3	3	3	3	3	0
n	30	43	30	30	19	156

Kruskal-Wallis 1-way ANOVA corrected for ties, H=10.70, $P<0.05$.

DISCUSSION

Nest density

Nest density had no effect on either hatching success per clutch or fledging success per brood. Other studies have found conflicting results. Parsons (1976), found that on the Isle of May, birds nesting at average densities bred more successfully than those nesting at either higher or lower densities. Kilpi (1989) studying a small colony between years found that in years of high nesting density, birds bred less successfully than in years of low nesting density. Hatching success was not affected by density; the difference between years was due to varying chick survival, which Kilpi and Parsons attributed to different levels of conspecific predation. Hunt and Hunt (1976) demonstrated this to be the case in Glaucous-winged gulls, showing that chick survival was inversely related to territory size and that this was due to neighbouring adults killing chicks. They suggested that there is a trade-off in territory size in gulls between the advantage gained from lower neighbour induced mortality at low nesting densities, and the disadvantage from inadequate colony defence against predators at low densities. To support this they cite the very large territory sizes of Western gulls on Santa Barbara Island, California, where predators are absent (Hunt and Hunt 1975). Their study also showed that the effect of territory size on chick survival only occurred in a year of low food availability when breeding success was low. This they suggested was due to the finding that "chicks that have failed to obtain food upon begging are more active and move further from their parents than recently fed chicks" (McLoon 1975 cited in HUnt and Hunt 1975). It is also presumably due to lower parental protection in years of low food availability, as the parents will be spending longer foraging, and to more birds relying on cannibalism in years when other food sources are reduced (Hunt and Hunt 1975).

On Sanda, no relationship between nest density and breeding success was found. A major difference between this study and that of Parsons, is that birds breeding on Sanda nested

at a far lower density than those on the Isle of May. Parsons showed that birds at very high densities and very low densities were less successful than birds nesting at average density. On Sanda, all of the birds nested at densities that were low by Parsons standards, so the lack of any relationship between nesting density and breeding success could be due to the small variation in density and the lack of birds nesting at high enough densities for killing of chicks by neighbouring adults to have a significant effect on chick survival.

Kilpi's study was slightly different to this study and those of Parsons and of Hunt and Hunt, in that he studied variation in breeding success and density at a small island colony between years. His findings could be partly due to the recruitment of first time breeders and inexperienced birds in years of high density. This would lower the average breeding success for seasons of high recruitment. Herring gulls that breed successfully at a colony are less likely to emigrate than those that are unsuccessful (Drost *et al.* 1961), so if these birds left only the more successful to breed in years of low nesting density, then on average, birds would be of a higher quality in years of low density than years when lots of freshly recruited birds were present. To negate this he argues that "many recruits were in fact not first-time breeders, and that production rates in high density years were not depressed by a large fraction of inexperienced breeders". However, in years of high recruitment (hence high density) breeding success was lower so this argument goes against his results. As evidence that these birds were not first-time breeders, he showed that they made no difference to mean laying date and clutch size. This may be true; however even if these birds were not first-time breeders, the fact that they have emigrated from another colony suggests that they were probably failed breeders in the preceding year and thus likely to be of lower than average quality. It would also be difficult to detect any trends in laying date and clutch size in his study as the maximum recruitment in any one year was only 12 pairs (from 32 to 44 pairs). It is interesting that in the year of maximum recruitment, the laying span of 90% of the pairs was longer than any other year, even than years when more pairs nested. This implies that recruits did breed later than usual and were therefore probably lower quality birds.

Nest cover

Nest cover had no influence on either hatching success per clutch or fledging success per brood. However, pairs with nest cover laid more eggs than pairs with no nest cover (Table 5.16). This is presumably not a causal relationship, but probably reflects less experienced birds choosing or being excluded by better competitors, to nest sites with no cover. Clutch size is on average smaller for inexperienced breeders or lower quality birds (see introduction to chapter 4).

Chick cover

Pairs with nests where cover was available for chicks, fledged more chicks per brood of 3 than those with territories with no cover (Table 5.18). Cover could affect chick survival in two ways; shelter from adverse weather conditions e.g. rainy windy conditions or hot calm weather, 'hiding holes' where chicks could escape predation or aggression from neighbours/siblings. All three forms of aggression were observed in the sample plots in 1989 however it was not possible to assess the relative importance of each. I have no evidence that inclement weather had any effect on chick survival in 1989, and during the chick-rearing period no periods of heavy rain, high winds or hot weather occurred.

The finding that differences in the amount of cover per nest in each sample plot could potentially explain the differences between sample plots in fledging success. However, mean cover per sample plot did not correlate with mean fledging success (Spearman rank correlation $r=0.10$, $n=8$, $P>0.05$), suggesting that the difference in fledging success was not caused by differences in availability of cover for chicks.

No measure of the physical differences between sample plots explain the differences in breeding parameters observed. It is possible that some other aspect of nest site quality could have produced this result, but it is difficult to imagine what this could have been.

Disturbance

Hunt (1972) showed that disturbance by humans could have an adverse effect on breeding success between colonies, but this seems unlikely to have been the case on Sanda. Sanda is uninhabited so the sample plots only received human disturbance from us routinely visiting them. All sample plots were visited in strict rotation, both for measuring eggs/chicks and collecting pellets so no differences in disturbance occurred through our visits. The only other large mammals that could possibly disturb the gulls were sheep (*Ovis aries*) which seldom ventured into the sample plots so it is thought that these had a negligible effect.

Sub-colony differences

The differences in breeding parameters found between the sample plots appear to be due to differences in the quality of the nesting birds themselves. Two breeding parameters that reflect adult quality are laying date and total clutch volume. These were both found to be different between the sample plots. In the Herring gull laying date has been shown to decrease with increased adult age until the birds are at least 11 years old (Davis 1975). This trend has also been shown to occur in other groups of birds e.g. Red-billed gulls *Larus novahollandiae* (Mills 1973), Kestrels *Falco tinnunculus* (Village 1986), Laysan Albatross *Diomedea* (Fisher 1969). As adult age/experience positively affects breeding success in gulls (e.g. Chabryzck and Coulson 1976) older birds are by definition of a higher quality. Age is however not the only factor affecting laying date in larids; within a cohort Red-billed gulls show variation in laying date that reflects differences in individual quality (as measured by Lifetime Reproductive Success (Mills 1989)). Any quality differences between sample plots in this study that were reflected in laying date could be due to age, individual quality, or a combination of the two. In this study, it was not possible to age breeding birds.

Egg volume has been found to correlate positively with reproductive success (Parsons 1972) as a result of both the direct advantage of extra provisioning in the egg and the

increased ability of birds laying large volume clutches (e.g. Bolton 1991). On Sanda in 1989 no relationship was found between individual egg volume or T.C.V. and breeding success. As this is taken as being due to high food availability negating the advantage normally gained by small chicks in receiving extra yolk from larger eggs (see chapter 5), any differences in T.C.V. can still be assumed to be a measure of adult quality as they reflect differences in the ability of adults to accrue reserves during the egg formation stage.

There was a significant relationship between laying date for each sample plot, and the mean fledging success per nest (Spearman Rank Correlation Coefficient, $r=-0.76$, $n=8$, $P<0.05$, Figure 5.2), indicating that the difference was due to the quality of birds nesting in each sample plot. Total clutch volume showed no such relationship (Spearman Rank Correlation Coefficient, $r=0.57$, $n=8$, N.S., Figure 5.3). One possible reason for this contradiction between the two measures of adult quality is that unlike laying date which shows an initial decrease with female age, T.C.V. does not. Davis (1975) found that T.C.V. increases with female age until 8 years old after which it declines. Unfortunately, in Davis' study he was not able to follow this trend in older birds. A review in Perrins and Birkhead (1987) shows that this trend does however continue with age in Chickens, Yellow-eyed Penguin (*Megadyptes antipodes*), Ruff (*Philomachus pugnax*), Kittiwake (*Rissa tridactyla*), Arctic Tern (*Sterna paradisaea*), Red-billed Gull (*Larus novaehollandiae*), Peregrine Falcon (*Falco peregrinus*) and Common Tern (*Sterna hirundo*), so as with Becker and Erdelen (1986) it is assumed here that there is at least no reversal of that trend in the Herring gull. In larids this age-related decline appears not to be associated with any decrease in breeding success (Mills 1989). If the sample plots on Sanda consisted of different aged birds, then one would expect colonies with older birds i.e. early layers, to be the most successful and for there to be a trend between sample plot success and laying date. If the average age in the sample plots containing older birds was greater than 8, then those with the oldest breeding birds would not have the highest average T.C.V. so any trend would be weakened. If there was no difference in mean age

Figure 5.2 Mean laying date and mean number of chicks fledged per 3-egg clutch, for the 8 sample plots on Sanda 1989.

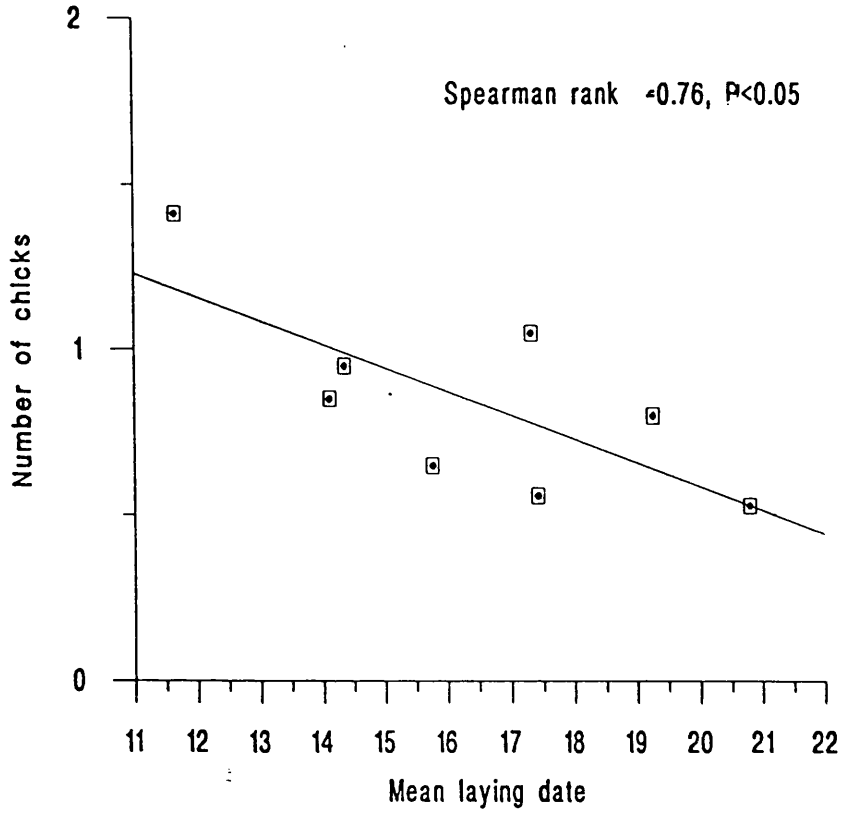
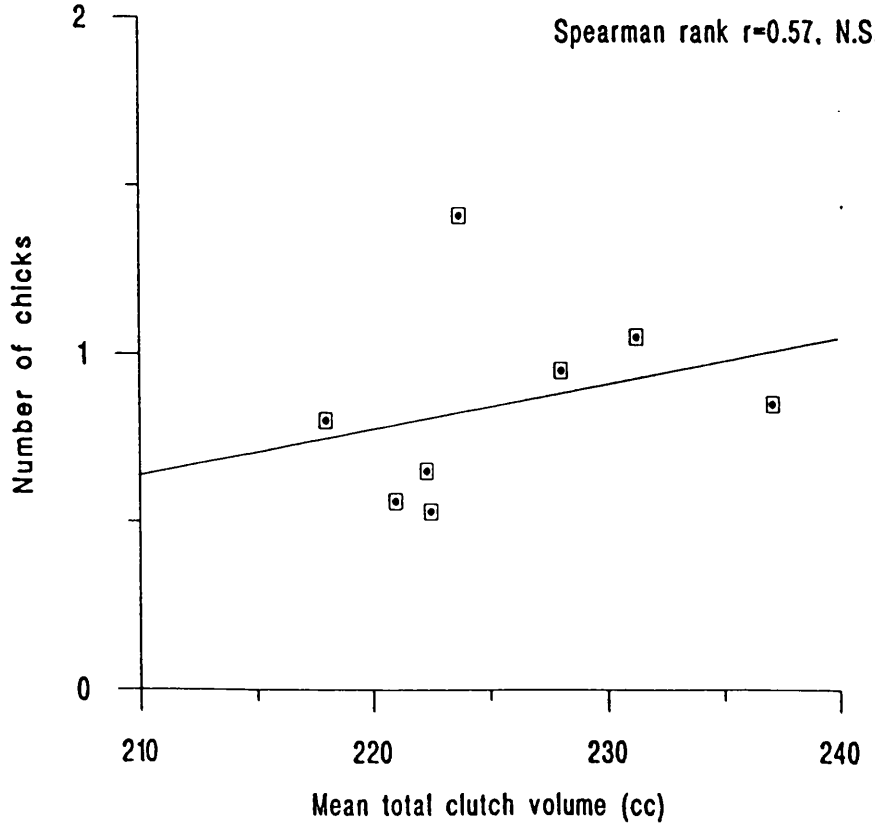


Figure 5.3 Mean total clutch volume and mean number of chicks fledged per 3-egg clutch, for the 8 sample plots on Sanda 1989.



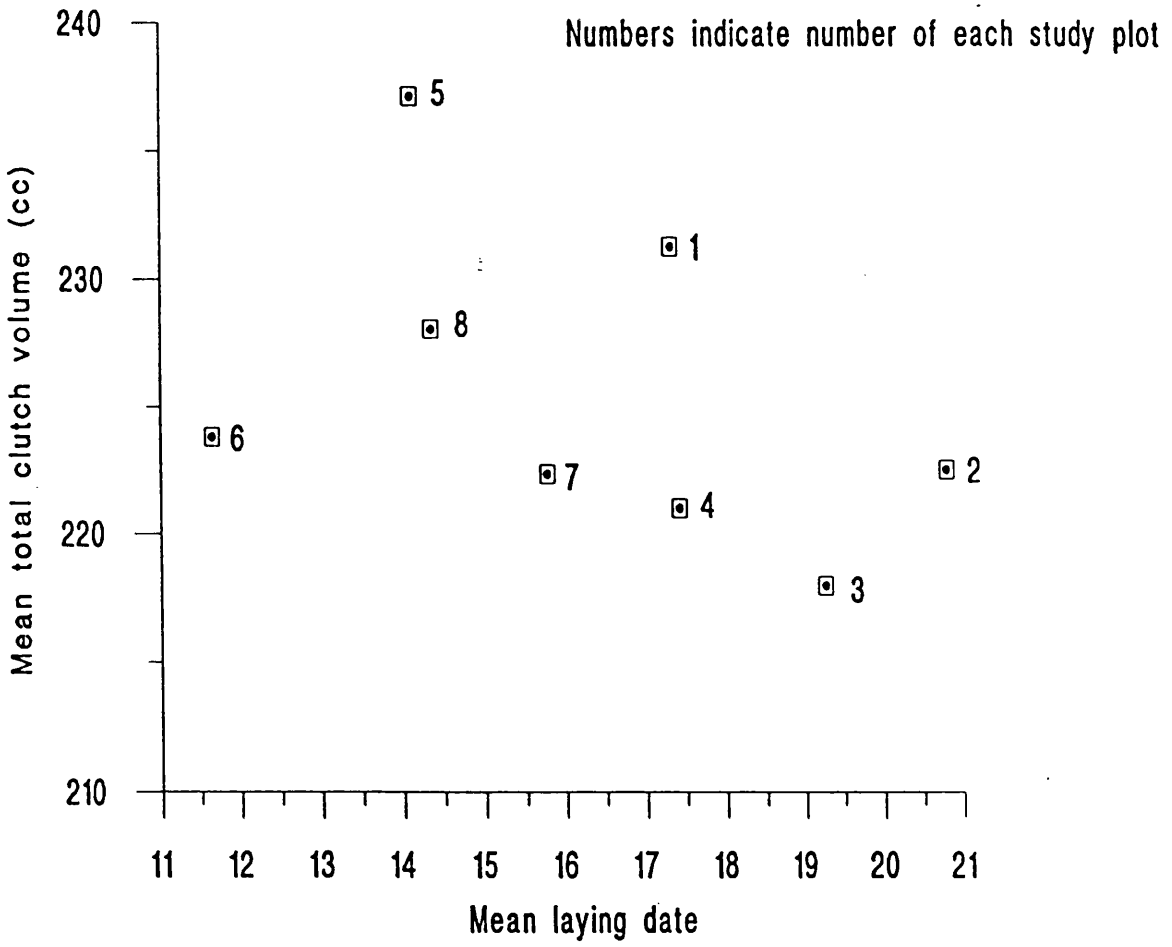
of birds between sample plots on Sanda, one would expect the quality differences as reflected by laying date and T.C.V. to relate to breeding success in the same way, as they are both measures of the ability of pairs to accrue reserves for egg formation and therefore presumably equal measures of quality.

Becker and Erdelen (1986) have shown in a colony where the pattern of expansion was known, that the combination of T.C.V. and laying date can be used to roughly assess the age structure of different areas of a colony. They found that in long-established areas of the colony, females laid smaller volume eggs than elsewhere and that they also laid them earlier. These females were therefore assumed to be old established breeders. In more recently colonised areas birds laid larger eggs later in the season except for one area where small eggs were laid very late in the season. The large egg layers were adjudged to be "middle-aged" and the very late small-egg layers "younger breeders".

The sample plots on Sanda did not fall neatly into these three categories, however a similar trend did seem to occur. Using laying date and T.C.V., the three categories used by Becker and Erdelen do all appear to have been present on Sanda (Figure 5.4). Plot 6 showed low T.C.V. and early laying dates suggesting that it contained older birds. Females in sample plots 5 and 8 laid large T.C.V. clutches at an intermediate date and were thus probably Becker and Erdelen's "middle-aged" birds. Sample plots 2, 3, 4 and 7 all laid small T.C.V. clutches late in the season and were presumably younger birds. Sample plot 1 shows a high T.C.V. but relatively late mean laying date. This sample plot was also enigmatic in that the mean fledging success was much higher than one would expect from the mean laying date (Figure 5.2). I can offer no explanation for this finding.

Becker and Erdelen's hypothesis does offer a plausible explanation for the observed differences in breeding parameters between sample plots on Sanda. It is further supported by the limited information I have on the pattern of colonisation of Sanda by Herring gulls. This information was gathered from the lighthouse keepers on Sanda, our

Figure 5.4 Mean total clutch volume with mean laying date for each study plot Sanda 1989.



local boatmen and ringers from the Clyde ringing group. Originally the gulls nested only in one small colony on the S.E. coast in the vicinity of the current sample plot 6. From here the colony expanded to cover the S.E. coast to sample plot 5 and thereafter sample plot 7. The time at which sample plot 8 and the other sample plots were established is not known however sample plots 2, 1 and 4 were all observed to have increased between my visits in 1988 and 1989 and probably represent areas of recent colonisation and rapid expansion. Little is known of sample plots 3 and 8 as these are situated in coves that are difficult to enter and of little interest to anyone but a gull biologist.

My findings support those of Becker and Erdelen and no other hypothesis would seem to explain my observed relationship and lack of relationship between laying date and breeding success and T.C.V. and breeding success respectively. However as the relationships between T.C.V., laying date and age are based only on the work of Davis (1975), further work with known-age birds is required before this technique can be verified.

The use of sample plots

The wide variation in measurements of all breeding parameters except clutch size, suggest that the results of studies using sample plots and than extrapolating to population level, must be viewed with considerable caution. This is especially true of studies where only a single plot was used (e.g. Paynter 1949). In this study, the areas of highest breeding success were also the areas of Sanda that were first colonised. This high success appears to be due to the greater average age of birds breeding in those areas, and not to the direct effects of nesting habitat. The areas of Sanda that were first colonised are the most difficult for people to reach, as they are situated at the base of cliffs. It would therefore be much easier in a study of Herring gull breeding success on Sanda, to concentrate on nesting areas at the North of the island. This would however underestimate average hatching success by up to 1.4 eggs per clutch of 3, and fledging success by up to 0.88 chicks per C3 (this latter figure is higher than the actual fledging success recorded in most studies (Table 6.2).

In estimating the breeding success of gulls on Sanda, simply calculating the mean of all the sample plots in this study is inappropriate, as these represent a large proportion of the comparatively small (219 pairs) and unsuccessful population of gulls nesting away from the East shore, and a small proportion of the large (1130 pairs) and successful population nesting on the East shore. A possible way to control for this bias is to calculate the number of chicks that total number of pairs nesting in the East colony would rear, using the means from the study plots in that area. One could then do the same for nesting pairs away from this area, add the totals together, and then divide by the total number of pairs nesting on Sanda. Using the colony mean for the proportion of 3-egg to 2-egg clutches and the counts of nesting pairs (see chapter 1), gives a population of 172 pairs that laid C3's outside the East colony, and 887 pairs that laid C3's in that colony. C3-laying pairs in the East colony, hatched 2.74 chicks and fledged 0.94 chicks per pair. This would mean that 887 pairs would hatch 2431 eggs and fledge 834 chicks. Calculating the same for pairs away from the East colony gives us 371 eggs hatched and 122 chicks fledged from 122 pairs. Adding the number of eggs hatched and the number of chick fledged, and then dividing by the number of 3-egg laying pairs gives an average hatching success of 2.65 chicks per pair, and a fledging success of 0.90 chicks per pair. This figure for hatching success is considerably larger than the sample plot overall mean of 2.35 chicks hatched per clutch of 3. The mean chick productivity of 0.9 chicks per C3-laying pair is similar to the sample plot mean of 0.84 chicks per C3-laying pair.

CHAPTER 6

COMPARISON OF POPULATION BREEDING PARAMETERS BETWEEN SANDA AND WALNEY

INTRODUCTION

The populations of Herring gulls at Sanda and Walney have both recently undergone large scale changes. Walney, in common with most Herring gull colonies in Britain, has recently undergone a dramatic decrease after a period of rapid increase, while the colonies of the Sanda group of islands showed a similar increase earlier this century but has not suffered the more recent decrease (see Chapter 1).

The cause of the general increase in Herring gulls this century has been attributed to two main changes in the gull's environment: cessation of human persecution and the increase in food availability through exploitation of new food sources such as fishing boats, rubbish tips, sewage outlets and fish factories (Harris 1970, Spaans 1971, Mudge 1978, Lloyd *et al.* 1991). The cause of the decrease in most of the species' range in Britain is less well understood.

Populations of a species are affected by three main parameters: natality, mortality and dispersal. Natality (*i.e.* the number of young produced per female per unit time) has been shown to be affected by several environmental and social factors in Larids including; timing of breeding (Brown 1967, Hunt and Hunt 1976), age (Chabryzk and Coulson 1976), weather (Hébert and Barclay 1986), food availability (Hunt 1972), predation (Paynter 1949), cannibalism (Brown 1967) and human disturbance (Hunt 1972). The aim of this part of the study was to assess the breeding success of the colonies at Sanda and at Walney to establish whether differences in the population changes between these two colonies could be explained by differences in breeding success. Several other studies of Herring gull breeding success have been made in Britain in populations that were stable (Darling 1938) or increasing (e.g. Harris 1964, Brown 1967, Parsons 1970, Davis 1975, Mudge 1978). Comparisons with these allow us to establish relatively how successful the two colonies were and whether changes in population at several sites could have been due to differences in breeding success.

Studies of mortality in the Herring gull over the period of decline have not been made so the contribution that adult mortality has made to the decline cannot be established. Studies have however been made of the breeding success of colonies where high adult mortality has been induced through culls. Coulson *et al.* (1982), studied the response of the gull population on the Isle of May to a massive cull i.e. man-made mortality. They found that the reduced breeding population showed increased egg volume, increased recruitment from fledged chicks and increased skeletal size of fledglings. These changes were attributed to density dependent factors such as food availability. This decrease in competition resulted not only in increases in egg and fledgling size, but also led to the average age of recruitment to the colony being reduced. Prior to the cull, third year birds were not recorded breeding at the colony; however after the cull small numbers of third-year birds did breed each year. Coulson *et al.* (1982), suggested that this lowering of mean age of recruitment to the colony was due to "density-dependent effects, all of which tend to compensate for the much increased mortality rate of adult Herring gulls". Duncan (1978), in a study of a culled population of moorland nesting gulls at Mallowdale Fell, found a high proportion of third year birds breeding (7% of 640 birds culled) this he attributed to the very low density at this colony which permitted them to breed. He suggested that "young gulls distinguished by sub-adult plumage find it harder to gain a territory within a dense colony". Third year birds only appear to be able to breed in established colonies where competition has been reduced by high adult mortality. For this reason the proportion of third year birds breeding at Sanda and Walney was recorded as a measure of the degree of intra-specific competition at each colony.

METHODS

On Sanda data were collected on; laying date, clutch size, clutch and egg volume, hatching success, chick survival, chick growth and nest density using the techniques described in Chapter 2. The Walney data mostly comprise data collected during experimental work i.e. control groups or nests monitored for potential use in experiments. For this reason the data set is less complete, but covers most measurable aspects of the year's breeding performance; laying date, clutch size, clutch volume (for three egg clutches only), hatching success, chick survival, chick growth and nesting density. These data were collected and analysed using the techniques described in Chapter 2.

Third year birds were identified using the plumage features listed by Monaghan and Duncan (1978) and Grant (1982). This method undoubtedly over-records presence of third year birds as some adults in a population retain certain features of third year plumage; however it was the method employed by Coulson *et al.* (1982) and Duncan (1978), so comparisons with their results will not be invalidated by biases introduced by this technique. Birds were checked for signs of immature plumage from a hide situated centrally in the study area at Walney. On Sanda hide watches were carried out in three sub-colonies (sub-colonies 1, 2 and 5). For all nests at both sites, both of the adults were seen simultaneously at the nest so all birds were definitely recorded.

RESULTS

Laying date

Laying date did not vary between Sanda and Walney (Table 6.1); however the spread of clutch initiation did ($F_{1,247}=3.614$, $P<0.01$). This was not due to the effect of combining several sub-colonies' data from Sanda, as all sub-colonies showed a greater spread than Walney (e.g. the sub-colony with least variance, number 8, $F_{1,183}=2.25$, $P<0.05$.)

Clutch size

The proportion of eggs in each clutch size category varied between Sanda and Walney (Table 6.2). Partitioning the degrees of freedom (following Siegel and Castellan (1988)) showed that this difference was not due to one particular category (C1 and C2 $X^2=4.73$, 1 d.f., $P<0.05$, C3 vs C1 and C2 combined $X^2=12.51$, 1 d.f., $P<0.01$). Herring gulls on Walney laid proportionally significantly more one and three egg clutches than did those on Sanda.

Clutch and individual egg volume

A and *b* eggs from three-egg clutches were larger on Walney than on Sanda (Table 6.3); however *c* eggs did not differ between the colonies. Total clutch volume (T.C.V.) was larger at Walney than at Sanda however this only approached significance i.e. $P<0.1$ (Table 6.3).

Hatching success

Hatching success on Sanda was high, with clutches of three hatching a mean of 2.35 chicks per nest (78% hatching success, n=147). Clutches of two hatched on average 1.43 chicks per clutch (71% hatching success, n=35). No chicks were hatched from the 4 one egg clutches so the overall hatching success was 77.5% (n=510).

Table 6.1 - Distribution of laying dates at Sanda 1989 and Walney 1990

Colony	Percentiles 0	25	50	75	100	x	sd	n=
Walney	30/4	3/5	5/5	8/5	20/5	6/5	3.93	161
Sanda	21/4	2/5	6/5	11/5	26/5	7/5	7.47	187

Comparison of laying date between colonies - Mann Whitney U=14135, N.S.

Table 6.2 - Clutch size distribution at Sanda 1989 and Walney 1990

Colony	n	1	2	3	X	sd
Sanda	186	4	35	147	2.77	0.41
Walney	271	8	17	245	2.88	0.47

Distribution of clutch sizes $X^2=17.10$, 2 d.f., $P<0.01$

Table 6.3 - Comparison of mean egg volumes and total clutch volume between clutches of three from Sanda 1989 and Walney 1990.

	Walney 1990			Sanda 1989			Results*	
Egg	n=	X	s.d.	n=	x	s.d	t~	P
A	62	79.50	6.79	97	77.21	6.17	2.19	0.030
B	50	78.53	5.89	86	76.22	7.80	1.98	0.051
C	52	72.29	6.15	103	70.90	5.75	1.39	0.167
Total Clutch Vol.	113	229.04	17.65	131	225.28	16.91	1.70	0.091

* Results are from Student t-test between each egg category.

Clutches of three on Walney, hatched on average 2.45 chicks (81.7% hatching success, n=60). This was not different from the hatching success of clutches of three on Sanda (Mann-Whitney U=4059.5, n_1=147, n_2=60, N.S.).

Chick growth rates

Mean growth rates for chicks from each colony, split by hatch order, are presented in table 6.4. and comparisons of mean growth rates are presented in Figures 6.1a to 6.1i.

On Sanda *a* and *b* chicks showed no difference in growth rate for either T.H.B. or weight (T.H.B. - $F_{1,262}$=0.50, N.S. weight - $F_{1,262}$=0.88, N.S.). *C* chicks on Sanda grew slower than *a* and *b* chicks for both T.H.B.(*a* vs *c* $F_{1,230}$=9.41, P<0.01. *b* vs *c* $F_{1,223}$=8.01, P<0.01) and weight (*a* vs *c* $F_{1,230}$=18.73, P<0.001. *b* vs *c* $F_{1,223}$=17.20, P<0.001).

At Walney *a* and *b* chicks did not differ in growth rates (T.H.B. - $F_{1,158}$=0.72, N.S. weight - $F_{1,158}$=0.25, N.S.); however *c* grew slower than *a* and *b* chicks for both T.H.B. (*a* vs *c* $F_{1,162}$=8.97, P<0.01. *b* vs *c* $F_{1,162}$=7.10, P<0.05) and weight (*a* vs *c* $F_{1,162}$=24.14, P<0.001. *b* vs *c* $F_{1,162}$=16.91, P<0.001).

Growth rates for *a* chicks did not differ between Sanda and Walney for T.H.B. or weight (T.H.B. - $F_{1,213}$=0.72, N.S. weight - $F_{1,213}$=3.41, N.S. Table 6.4). *B* chicks showed no difference for either measure (T.H.B. - $F_{1,206}$=0.09, N.S. weight - $F_{1,206}$=0.12, N.S. Table 6.4). *C* chicks also showed no difference in growth rate between the two colonies (T.H.B. - $F_{1,178}$=0.07, N.S. weight - $F_{1,178}$=0.04, N.S. Table 6.4).

Chick survival

No differences between Sanda and Walney were found for survival of *a* or *b* chicks (X^2

Table 6.4 - Comparison of growth rates between chicks from broods of three from Sanda 1989 and Walney 1990

		Sanda 1989			Walney 1990			Difference	Significance*
Measure	Chick	n=	r=	b=	n=	r=	b=		
Head + Bill (mm/day)	A	69	0.985	1.98	42	0.986	2.03	0.05	N.S.
	B	69	0.986	1.95	42	0.984	1.97	0.02	N.S.
	C	69	0.978	1.80	42	0.984	1.78	0.02	N.S.
Weight (g/day)	A	69	0.962	29.1	42	0.965	30.8	1.7	N.S.
	B	69	0.973	28.6	42	0.972	29.0	0.4	N.S.
	C	69	0.960	24.5	42	0.959	24.8	0.3	N.S.

n= sample size
r= correlation coefficient
b= slope from regression equation
Growth rates taken from chicks between 5 and 25 days post-hatch.

* Covariance results from MANOVA test for differences between slopes for each group (Anon. 1988).

Figure 6.1c Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "b" chicks from Sanda 1989 and Walney 1990.

Figure 6.1d Comparison of rate of weight gain from 5 to 25 days post-hatch between "b" chicks from Sanda 1989 and Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.

Figure 6.1c Sanda "b" chicks with Walney "b" chicks.

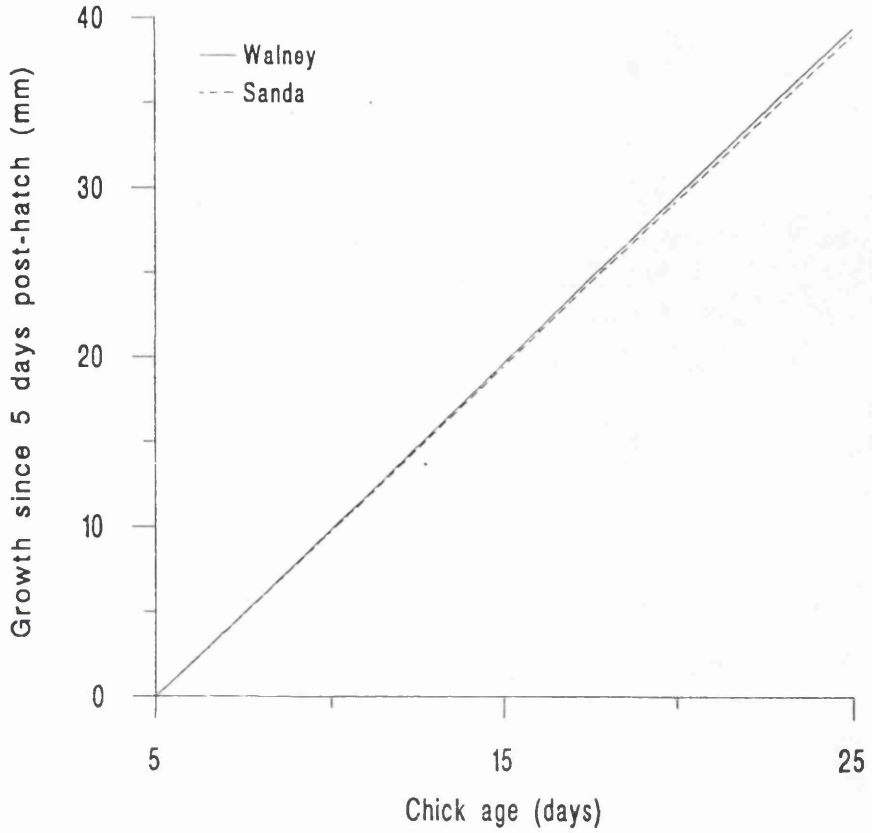


Figure 6.1d Sanda "b" chicks with Walney "b" chicks.

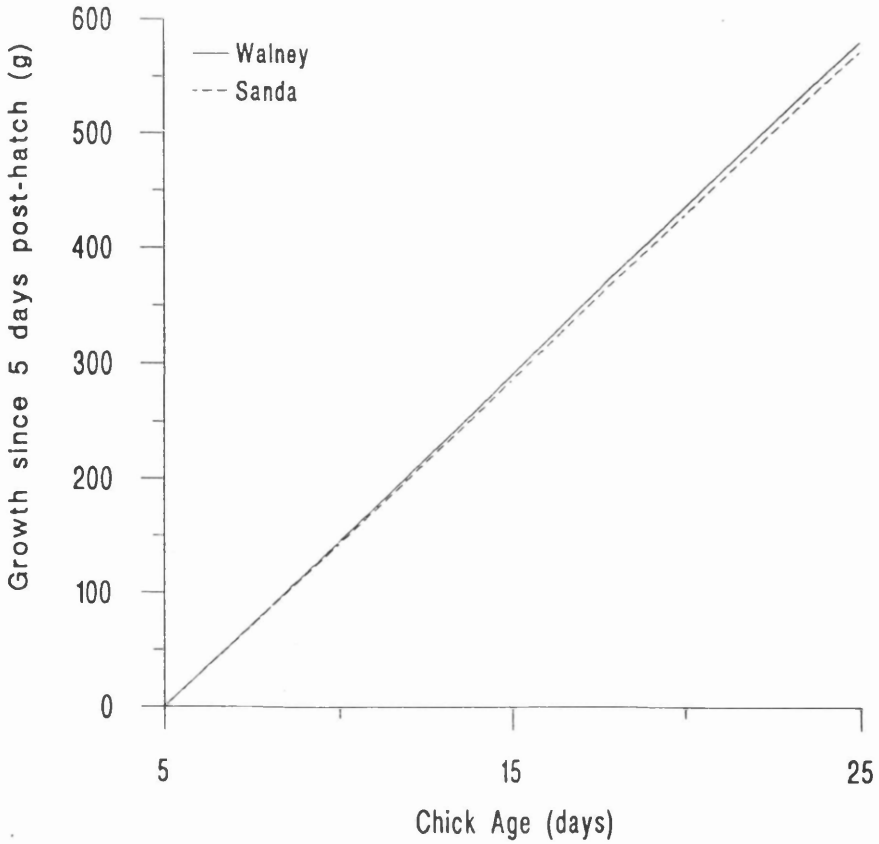


Figure 6.1e Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "c" chicks from Sanda 1989 and Walney 1990.

Figure 6.1f Comparison of rate of weight gain from 5 to 25 days post-hatch between "c" chicks from Sanda 1989 and Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.

Figure 6.2e Sanda "c" chicks with Walney "c" chicks.

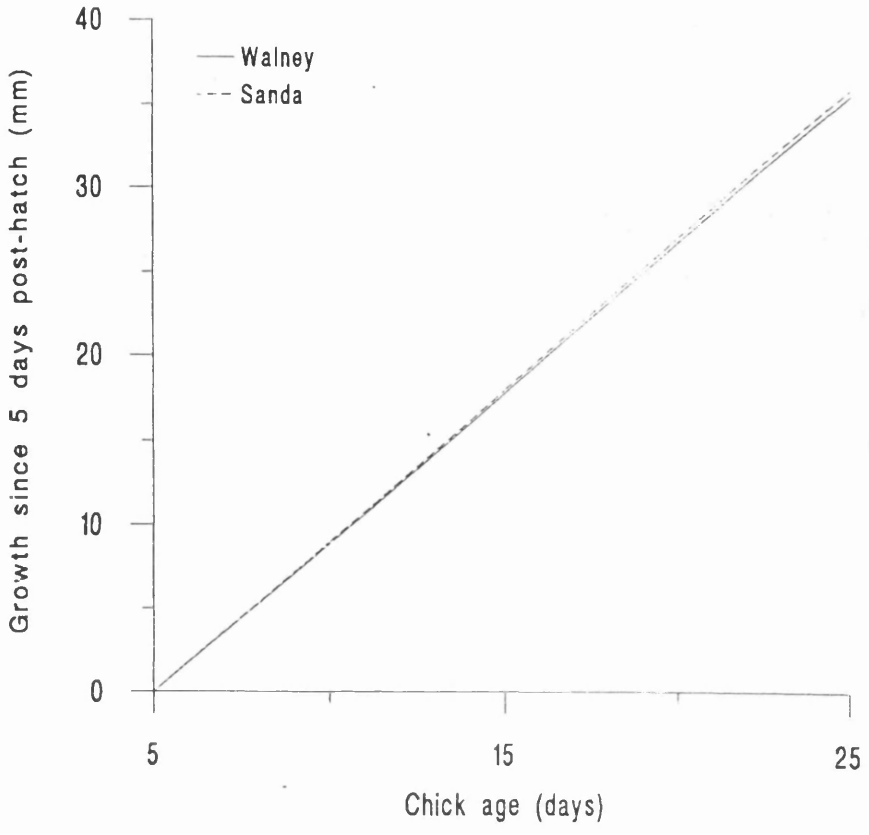


Figure 6.1f Sanda "c" chicks with Walney "c" chicks.

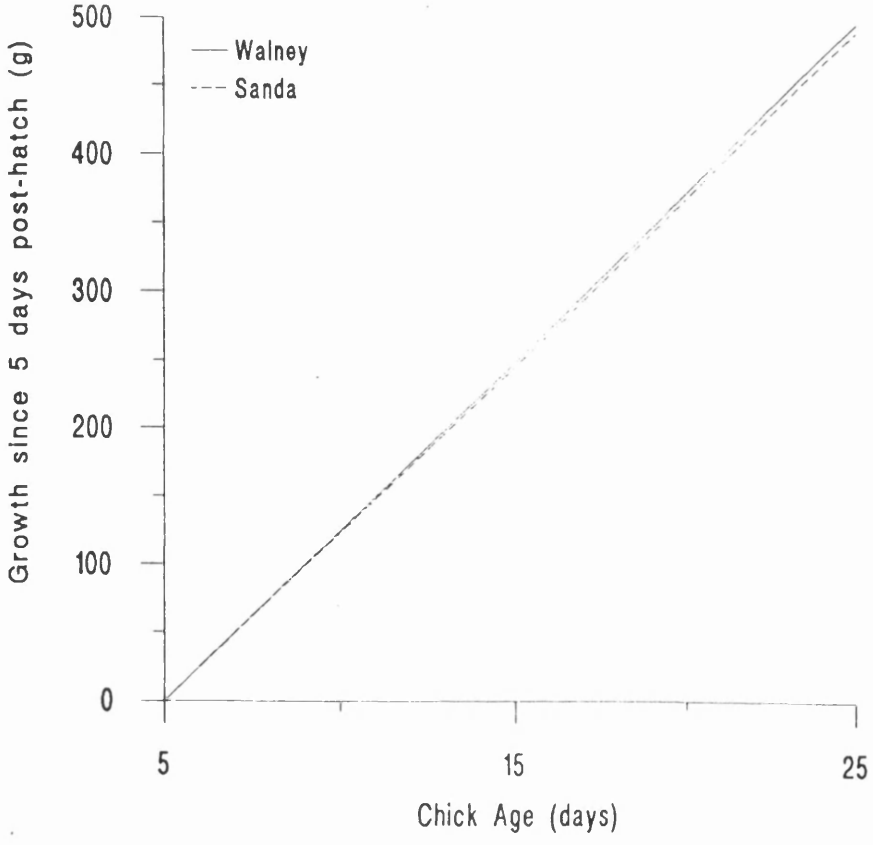


Figure 6.1g Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between chicks by hatch order, Walney 1990.

Figure 6.1h Comparison of rate of weight gain from 5 to 25 days post-hatch between chicks by hatch order Walney, 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.

Figure 6.1g Walney - all chicks

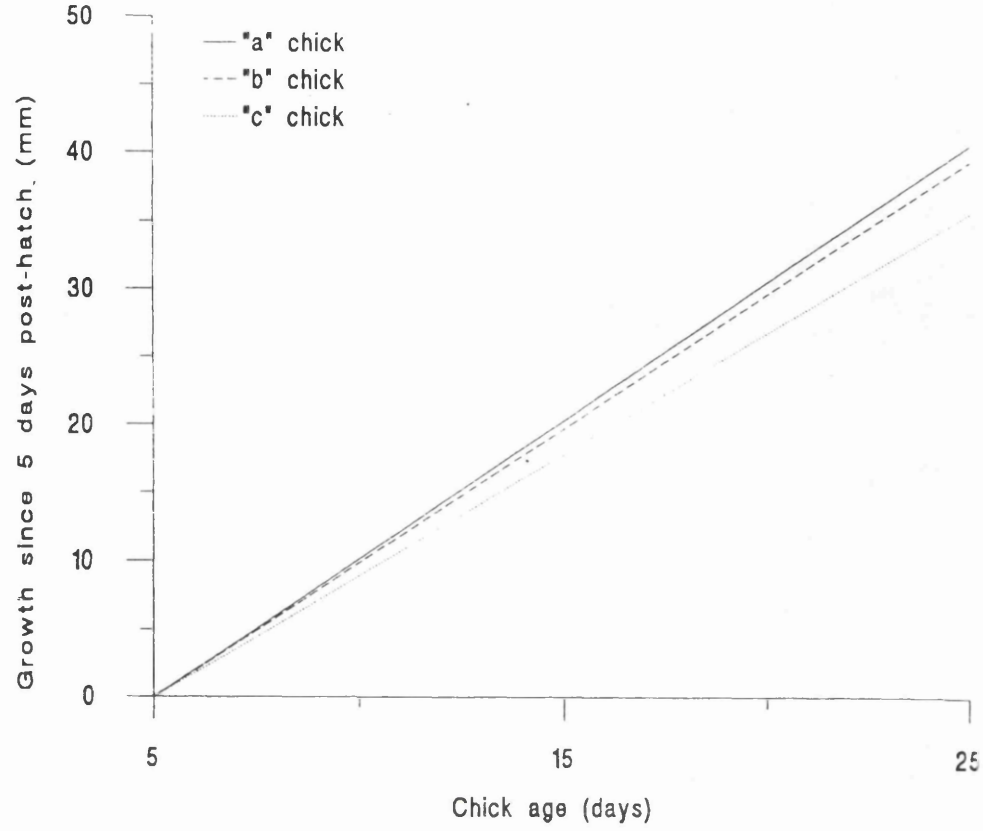


Figure 6.1h Walney - all chicks

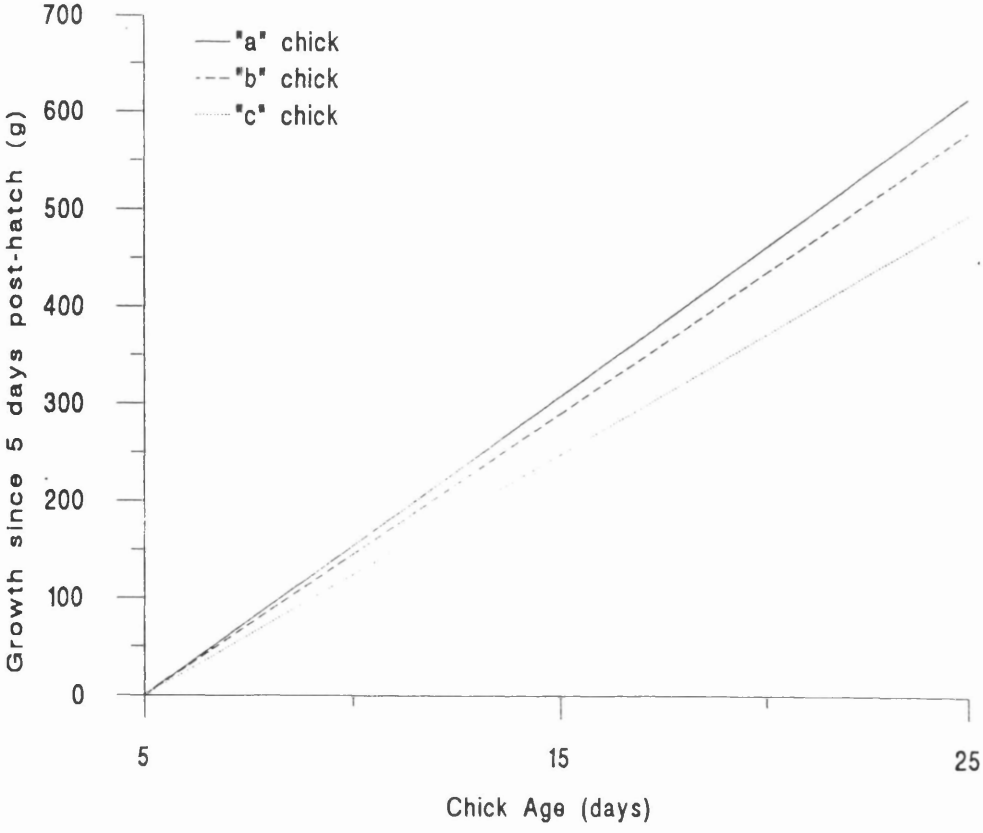


Figure 6.1i Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between chicks by hatch order, Sanda 1989.

Figure 6.1j Comparison of rate of weight gain from 5 to 25 days post-hatch between chicks by hatch order Walney, 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.

Figure 6.1i Sanda - all chicks

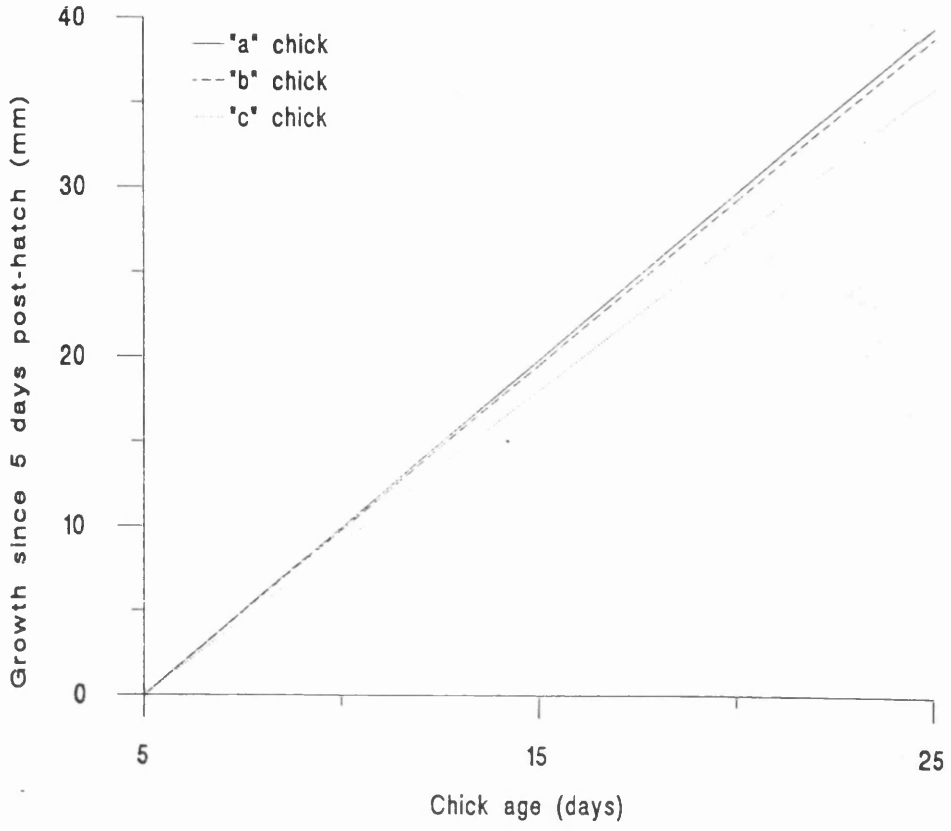
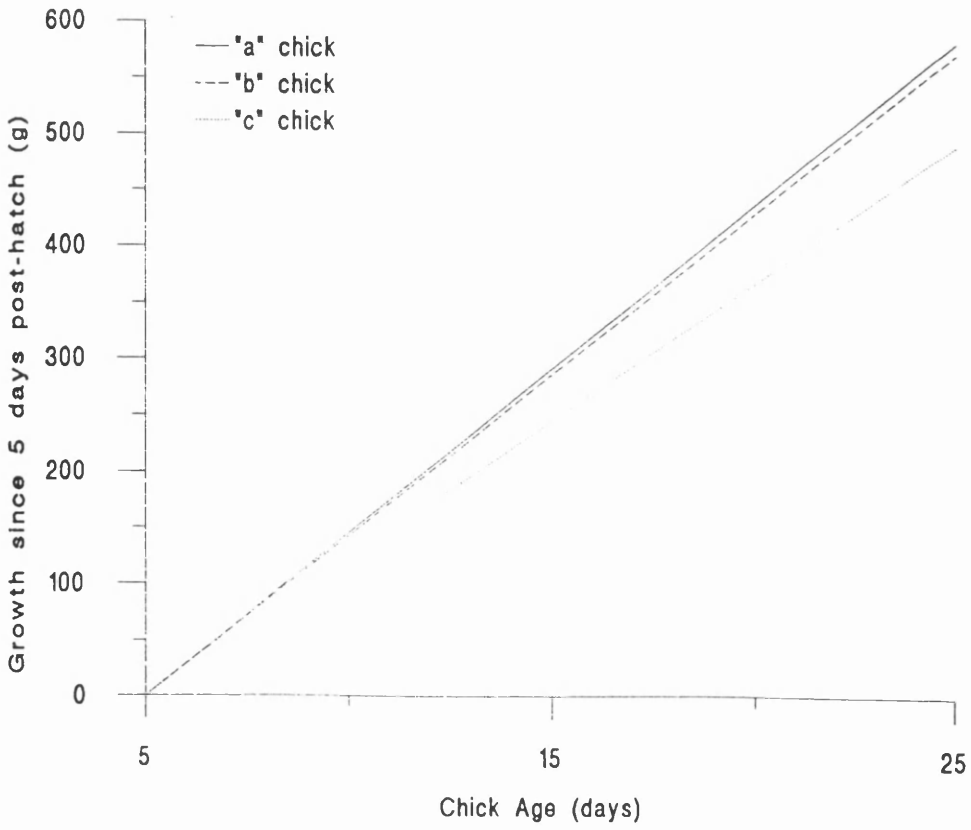


Figure 6.1j Sanda - all chicks



with Yates' correction = 0.15 and <0.01 respectively, d.f. 1, N.S. Table 6.5). However there was a difference in *c* chick survival between colonies, with a greater proportion (20.7%) of *c* chicks surviving to four weeks post-hatch at Walney than at Sanda (X^2 with Yates' correction = 6.52, P<0.05. Table 6.5).

The mean number of chicks fledged per brood of three was not different between Sanda (0.84 chicks per brood of 3, n=69), and Walney (0.88 chicks per brood of 3, n=42) (Mann-Whitney U=1348.5, n_1=69, n_2=42, N.S.).

The timing of chick mortality was different between Sanda and Walney for *a* or *b* chicks, with higher mortality during the first week post-hatch at Sanda (Figures 6.2a-6.2b). *C* chicks, showed no difference in the pattern of timing of mortality (Figure 6.1c).

Within colonies, hatching order had no effect on chick survival at Walney (X^2=0.536, 2 d.f., N.S.) but did at Sanda (X^2=10.89, 2 d.f., P<0.01). This was due to the low survival of *c* chicks on Sanda (partitioned degrees of freedom following Siegel and Castellan (1988) *a* and *b* combined versus *c* - X^2=10.87, 1 d.f., P<0.01).

Breeding density

The breeding density as measured by the number of neighbouring nests within 5 metres of sample nests, did not differ between Sanda and Walney (Table 6.6).

Proportion of breeding birds in immature plumage

No birds were observed breeding in sub-adult plumage at Sanda, although sub-adults were observed around the colony on most visits. At Walney, of 92 breeding birds, 12 (13%), were breeding in sub-adult plumage. At Sanda no third year birds were observed breeding at the 98 nests observed over a period of two weeks.

Table 6.5 - Cumulative Mortality of chicks from broods of three/ Sanda 1989 and Walney 1990

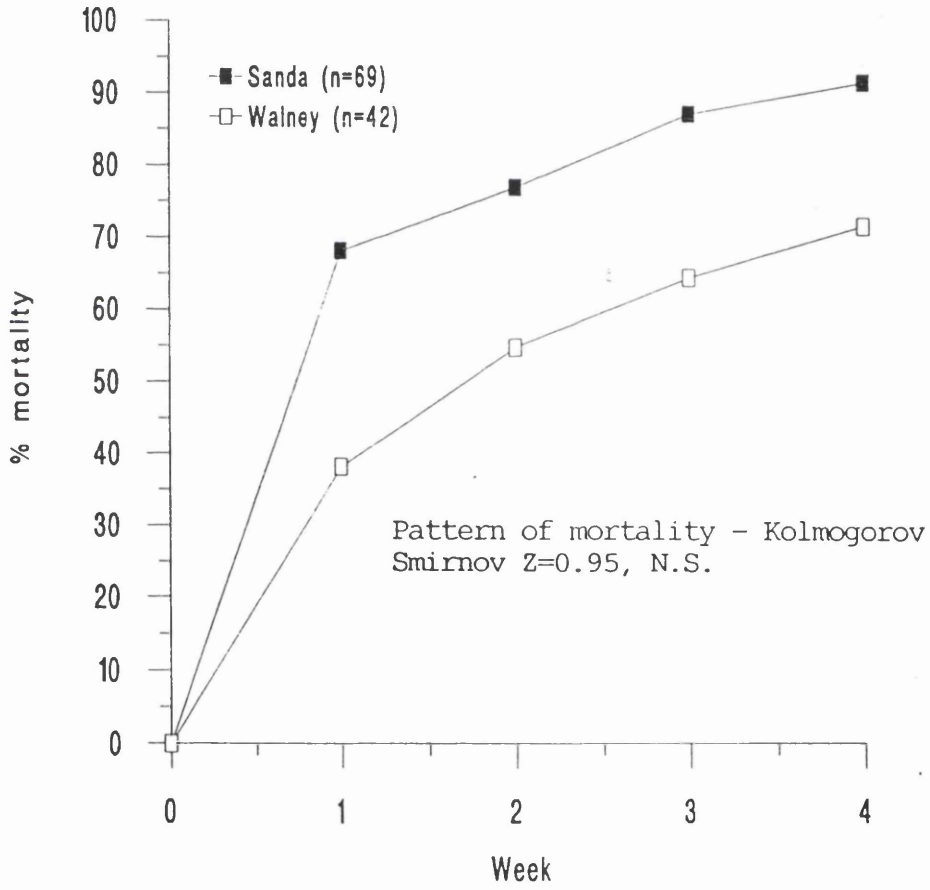
Colony	Chick	n=	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
Walney	A	42	4 (9.5)	17 (40.5)	21 (50.0)	28 (66.7)
	B	42	4 (9.5)	23 (54.8)	25 (59.5)	31 (73.8)
	C	42	16 (38.1)	23 (54.8)	27 (64.3)	30 (71.4)
	All	126	24 (19.0)	63 (50.5)	73 (57.9)	89 (70.6)
Sanda	A	69	23 (33.3)	32 (46.4)	39 (56.5)	50 (72.5)
	B	69	23 (33.3)	38 (55.1)	41 (59.4)	50 (72.5)
	C	69	47 (68.1)	53 (76.8)	60 (87.0)	63 (91.3)
	All	207	93 (44.9)	123 (59.4)	140 (67.6)	163 (78.7)

Table 6.6 Frequencies of neighbours within 5 metres of sample nests at Sanda 1989 and Walney 1990

Colony	Nests within 5m 0	1	2	3	4	5+	n=	Mean	Median
Sanda	4	6	7	8	9	8	42	2.57	2.0
Walney	2	2	9	4	2	1	20	2.25	2.0

Comparison of number of neighbours within 5 metres of sample nests at each colony- Mann-Whitney U= 568.0, N.S.

Figure 6.2c Cumulative mortality of "c" chicks from Sanda 1989 and Walney 1990 from 1-4 weeks post-hatch.



The proportion of birds breeding in immature plumage was different between Sanda and Walney (X^2 with Yates' correction = 23.54, P<0.001), although use of a X^2 test in this case is not advisable (Siegel and Castellan 1988) as one expected value is less than 5 (although see Snedecor and Cochran (1967) who suggest that expected values of >1 are acceptable as long as they represent less than 25% of the cells), it is obvious that a difference occurred between the colonies (if the Sanda sample was halved, the use of this test would be valid and the difference between the colonies would still be significant i.e. X^2 with Yates' correction = 11.53, P<0.001).

Comparison of breeding success and other parameters with other studies

Clutch size

The clutch sizes at both Walney and Sanda were high compared with other published data for British colonies (see Table 6.7). All other studies were made at increasing colonies; however in spite of the seemingly good conditions for breeding at each of these colonies, none had higher mean clutch sizes than the decreasing colony at Walney.

Hatching success

Both the colony at Sanda and the colony at Walney enjoyed higher hatching success than in any other published studies other than the results of Darling (1938) for the Summer Isles in N.W. Scotland (Table 6.8). The proportion of eggs that hatched was higher on Walney in 1990 than in 1965 (X^2 with Yate's correction =38.78, 1 d.f., P<0.001). However, Brown's figures for hatching success presumably included 1 and 2-egg clutches, the eggs from which are less likely to hatch than those from C3's (Harris 1964, chapter 4). Brown does not give details for the clutch size distribution from his sample; however he does for a sample of nests on Walney during his study (Table 6.7). He found that 63.3% of clutches were C3's, 29.4% C2's and 7.2% C1's. This means that 73.4% of eggs in a random sample of nests would be in clutches of three, with 22.7% in C2's and 3.9% in

Table 6.7 - Reported clutch sizes and clutch size frequencies from British Herring gull colonies

Colony	Year	n=	clutch sizes 1	2	3	Mean	Reference
Skomer	1962	220	13	27	180	2.76	Harris 1964
Walney	1962 -65	139	10	41	88	2.56	Brown 1968
I.o.May	1968	-	-	-	-	2.73	Parsons 1971
Skokholm	1970	-	-	-	-	2.69	Davis 1975
Skokholm	1972	-	-	-	-	2.61	Davis 1975
Sunderland	1975	13	-	-	-	2.5	Monaghan 1979
South Shields	1975	14	-	-	-	2.6	Monaghan 1979
Sanda	1989	186	4	35	147	2.77	This study
Walney	1990	271	8	17	245	2.88	This study

Table 6.8 - Comparison of hatching success at Sanda 1989 and Walney 1990, with other published data.

Colony site	Year	Hatching success	n=	Reference
Summer Isles	1936	86.0%	40*	Darling (1938)
" "	"	84.5%	12*	"
" "	"	87.5%	7*	"
" "	1937	95.7%	65*	"
" "	"	89.0%	3*	"
Dungeness	1952-56	25-30%	266	H.E. Axell (cited in Davis)
Skomer	1962	63.0%	220	Harris (1964)
Walney	1962-65	52.0%	250	Brown (1967)
I.o.May	1968	75.0%	2470	Parsons (68)
Skokholm	1970	72.0%	366	Davis (1975)
"	1972	65.4%	224	"
Sunderland	1975	42 %*	13	Monaghan (1979)
South Shields	1975	44 %*	14	Monaghan (1979)
Sanda	1989	77.5%	510	This study
Walney	1990	81.7%	180[a]	This study

* indicates that sample size refers to number of nests not eggs
[a] hatching success figures for Walney were taken only for a sample of three-egg clutches

C1's. If in Brown's study 81.7% of eggs in C3's hatched (the hatching success that I recorded), then even if only 10% of those in C2's hatched, then the hatching success would have been 62.4% which is significantly higher than that recorded by Brown (X^2 with Yates' correction = 5.11, 1 d.f., $P<0.05$).

Egg volumes

Individual egg volumes and T.C.V. were larger than the published figures for all studies except those for the Isle of May *post* cull (figures for 1974 onwards, Table 6.9). The volumes of Sanda eggs were similar to those found on the Isle of May in 1968, before the culling was started.

Chick survival

A wide range of levels of fledging success have been recorded at British colonies (Table 6.10). The levels of fledging success recorded at Sanda and Walney were higher than those published for Skomer however considerably lower than those for the Isle of May and Brown's earlier study at Walney (Brown 1967). This is in spite of the fledging success at Walney being recorded for 3 chick broods only and thus probably being an overestimate of fledging success for the colony as a whole. The fledging success at Sanda and at Walney were both considerably lower than those found by Monaghan (1979) at roof-top colonies at Sunderland and South Shields.

Nest density

The only comparable data on nesting density come from Parsons (1968). Due to the categories employed by Parsons, a statistical comparison could only be made with his data by combining both Sanda and Walney data, as he found very few pairs nesting at such low densities as those found at Sanda and Walney. As the nesting densities were not different between Sanda and Walney (Mann Whitney $U=568.0$, $n_1=20$, $n_2=42$, N.S.), I felt that this was valid to show any gross difference between the studies. Parsons measured density by counting the number of pairs nesting within 15 feet of any given nest, as opposed to 5

Table 6.9 - Comparison of individual egg and clutch volumes (cm3) between Sanda 1989, Walney 1990 and published data

Study site	Sanda	Walney	Skomer	Skok.	Skok.	Skok.	I.o.M.	I.o.M.	I.o.M.	I.o.M.	I.o.M.
Year	1989	1990	1962	1969	1970	1972	1968	1974	1975	1976	1977
a egg volume	77.21	79.50	76.29	76.06	76.45	76.26	77.92	80.99	79.73	80.94	81.48
S.E.	0.63	0.86	-	0.48	0.43	0.52	0.29	0.34	0.46	0.55	0.48
(n=)	(97)	(62)	(100)	(122)	(215)	(116)	(455)	(85)	(90)	(72)	(135)
b egg volume	76.22	78.53	76.60	75.45	73.78	74.11	76.12	76.59	75.30	76.73	78.38
S.E.	0.84	0.83	-	0.48	0.43	0.52	0.29	0.30	0.40	0.51	0.56
(n=)	(86)	(50)	(100)	(122)	(215)	(116)	(455)	(84)	(90)	(72)	(135)
c egg volume	70.90	72.29	67.85	68.31	67.31	66.88	69.32	72.75	71.66	71.55	73.42
S.E.	0.57	0.85	-	0.48	0.43	0.57	0.30	0.32	0.48	0.48	0.51
(n=)	(103)	(52)	(100)	(122)	(215)	(116)	(455)	(84)	(90)	(72)	(135)
Total clutch volume	225.28	229.04	220.74	219.82*	217.54*	217.25*	223.36*	230.33*	226.69*	229.22*	233.28*
S.E.	1.48	1.66	-	-	-	-	-	-	-	-	
(n=)	(131)	(113)	(100)	(122)	(215)	(116)	(455)	(84)	(90)	(72)	(135)
Reference	This study	This study	Harris (196?)	Davis (1975)	Davis (1975)	Davis (1975)	Parsons (1971)	Duncan (1978)	Duncan (1978)	Duncan (1978)	Duncan (1978)

* indicates total clutch volume calculated by addition of individual egg volumes, actual values not published.

Table 6.10 - Published levels of chick survival at British Herring gull colonies

Study site	Year	Survival per brood (n=)	Survival per chick (n=)	Reference
Summer Isles	1936 -37	-	0.12-0.49	Darling (1938)
Skomer	1962	0.14 (220)	-	Harris (1964)
Walney	1965	-	0.54 (224)	Brown (1968)
Skokholm	1970	0.6	0.31	Davis (1975)
Sunderland	1975	1.58	-	Monaghan (1979)
South Shields	1975	1.59	-	Monaghan (1979)
I..o. May	1978 -79	1.32 (170)	-	Graves et. al. (1984)
I. o. May	1980	1.26 (20)	-	Graves et. al. (1984)
Sanda	1989	0.84[1] (147)	0.79[2] (207)	This study
Walney	1990	0.88[1] (126)	-	This study

[1] = indicates survival from broods of three
[2] = indicates survival from clutches of three

Table 6.11 - Comparison of the nesting densities of Herring gulls on the the Isle of May 1968, and Walney and Sanda (1989 and 1990 respectively).

Colony	Nests within 5m 0-1	2-3	4+	Mean	n=
Sanda + Walney	14	28	20		62
(%)	(22.6)	(45.2)	(32.3)		
I.o.May*	10	42	159		211
(%)	(4.7)	(19.9)	(75.4)		

Difference between colonies $X^2=42.58$, 2 d.f., $P<0.01$.
* Data from Parsons 1975

metres in this study thus, his categories (See Table 6.11) should include less birds on average if the gulls on the Isle of May were nesting at the same density as on Sanda and Walney. In spite of this, a comparison with his data show that nesting density was lower on Sanda and Walney than on the Isle of May (Table 6.11). Partitioning the degrees of freedom (following Siegel and Castellan 1988), shows that this was due to more birds nesting in the 4+ category then the others ($X^2=39.24$, 1 d.f., $P<0.01$, comparison of categories 0-1 and 2-3; $X^2=2.43$, 1 d.f., $P>0.05$).

Number of birds breeding in third-year plumage

The proportion of birds breeding on Walney in third year plumage was higher than the highest proportion found by Coulson *et al.* (1982) for the Isle of May (2.79% of 430 birds in 1977, X^2 with Yates' correction = 15.89, 1 d.f., $P<0.001$) and not different from that found by Duncan (1978) at Mallowfield Fell (7% of 640 birds, X^2 with Yates' correction = 3.26, 1 d.f., N.S.).

DISCUSSION

Laying date

Whilst the laying date between Sanda and Walney was not different, there was a difference between colonies in the spread of clutch initiation (the distribution of laying dates for the first laid egg in each clutch). The gulls in the colony at Walney initiated laying more synchronously than either the total Sanda population or any of the sub-colonies studied. The finding that colonially nesting species tend to synchronise clutch initiation has been documented in several species and is normally referred to as the "Fraser Darling" effect. Darling (1938) suggested that the phenomenon of synchronous clutch initiation in colonial birds was due to "social stimulation" whereby birds whose neighbours are displaying and nest building will be stimulated by the activity around them and breed at the same time. Since Darling, many other studies have shown that colonially nesting birds exhibit this type of nesting synchrony, although the adaptive function, and the possibility that synchrony could be produced by other factors e.g. age structures of

colonies, has not been conclusively tested (see Gochfield 1980 for a full review). Strong evidence for "Fraser Darling" effect occurring in Herring gulls has been provided by Parsons (1976) and Burger (1979). Parsons showed that within a large colony, birds within an area showed synchronised laying. Burger expanded this work and showed that as colony size increases, so does the degree of laying synchrony (as measured by the standard deviation of mean laying date of the first egg in a clutch). This relationship between colony size and synchrony breaks down in colonies with over 250 pairs "thereafter the group size was so large that individuals no longer interacted with the whole group, but began to interact in smaller groups".

The study plot on Walney was in one area where all of the birds at study nests could see each other. The difference between the degree of synchrony in the sample plots at Sanda, and the sample plot at Walney could be due to "Fraser Darling" effect, with increases colony size resulting in increased synchrony. This would not however explain the difference between Walney and the study plots on the East coast of Sanda, where far more than Burger's 250 pair threshold nest. The difference between this area and Walney appears to be more due to habitat than to numbers of nesting neighbours. On Sanda the gulls nest in boulder beach areas where most incubating or often even displaying birds, are visually isolated from each other. During the early part of the breeding season, the gullery at Walney is on mostly on open short grassed dunes, where birds can see literally hundreds of other nesting pairs. Burger suggested that "vegetation may also influence social facilitation. Gulls nesting in dense cattails or tules might have smaller areas of synchrony than those nesting in the open, such as the Herring gulls on grassy knolls at Walney". She argued that this would be the case due to a reduction in the number of pairs that any one pair can see from their nest sites. In the case of this study, the difference would appear to be due to differences in visibility as a result of different nesting substrates rather than vegetation.

Clutch size

Differences in clutch size were found between Sanda and Walney, with the colony at

Walney containing proportionally more 1 and 3 egg clutches. The increased proportion of 3-egg clutches presumably reflects higher food availability for pre-laying gulls at Walney, as clutch size is known to be higher in years of high food availability (Davis 1975) or in years when conditions allow easy access to food (Darling 1938). The higher proportion of 1-egg clutches does not appear to support this interpretation, although the number of birds with 1-egg clutches at each colony represent a very small proportion of the total nesting attempts. At Sanda it was found that 1-egg clutches hatched no chicks at all and when the eggs were inspected during routine visits, the eggs were found to be cold and no incubating birds were seen at any of the nests. It seems likely therefore that at least some of the 1-egg clutches represent partially-predated clutches or nesting attempts that were abandoned after one egg had been laid. This interpretation has also been suggested by Harris (1964) who found that of 13 1-egg clutches, none hatched. The amount of cover for nests is very different between the colonies at Sanda and Walney, with the colony at Sanda being situated amongst boulders with nests being less visible and less accessible to marauding gulls than the nests at Walney which are mostly situated in a well grazed dune system with very little cover. The colony at Walney also suffers greater disturbance by people and particularly cattle which often flush incubating adults, leading to more opportunities for predation to occur. Brown (1967) noted that the level of con-specific egg predation at Walney was very high.

Comparison with other studies show that the mean clutch sizes for both Sanda and Walney were very high. It is particularly interesting to find that the two highest mean clutch sizes recorded are for Priest Island (Darling 1938) and Walney 1990, a stable colony and a decreasing colony respectively. All other colonies for which clutch size data are available were increasing at the time of study. Chabryzk and Coulson (1976), showed that young birds ($\leq$6 years old) lay smaller clutches than older breeders (>6 years old). A possible explanation for the small average clutch size found in rapidly expanding colonies, could be that these populations consist of a large proportion of young breeders. However, the large proportion of birds breeding in immature plumage at Walney suggests that this is

not the reason for the differences in clutch size between this study and studies at expanding colonies. Coulson *et al.* (1982) showed that decreasing the number of nesting birds at a colony increases the mean clutch size; this appears a more likely explanation for the difference between the studies. Clutch size has also increased at Walney since 1965 when the colony was still increasing and the nesting population was much larger (Brown 1967).

Egg and clutch volume

Total clutch and *c* egg volumes did not differ between Sanda and Walney, however *a* and *b* eggs were larger at Walney. The volumes at both colonies were large by comparison to previous studies, with only the Isle of May colony having recorded larger eggs. Coulson *et al.* (1982), showed that this was due to a reduction in the number of pairs breeding at the colony by culling, and interpreted the increase in egg volumes as being due to reduced competition for food. Egg volumes on the Isle of May prior to the cull were slightly smaller than those from either Sanda or Walney. The large egg sizes at these colonies suggest that nesting adults had little difficulty in finding food prior to laying.

Hatching success

Hatching successes were not different between Walney and Sanda either in terms of hatching success per egg or number of chicks hatched per brood. At Walney, hatching success was only recorded for clutches of three. This means that clutches that were partly or totally depleted during laying were not included, resulting in an overestimate of hatching success. If birds whose eggs were removed during laying were of a lower average "quality" than those that completed their clutches, then this omission could also increase the average quality of the sample of 3-egg parents and thus introduce a further overestimate of fledging success. It is not possible to estimate how large these introduced biases were; however it seems unlikely that many clutches would be depleted during egg-laying, as full incubation commences with the laying of the second egg (2 days after clutch initiation) and after this, predation probably occurs at the same rate as during the rest of

incubation. Compared with other studies these hatching successes were extremely high, with only the figures for Summer Isles 1936-37 exceeding them. The main cause of failure to hatch is predation, mostly by con-specifics (e.g. Harris (1964), Brown (1967) and Parsons (1971)). This can be indirectly affected by food availability in that in years of low food availability, adults spend more time foraging and thus can put less effort into protecting the clutch (Hunt 1972). It also seems likely that the level of cannibalisation would increase as other food sources become less available.

Chick growth and survival

No differences were found between the growth rates of *a*, *b* and *c* chicks between the two colonies however, the *c* chicks grew slower than their siblings at both colonies. *C* chicks at Sanda gained 4.1g and 4.6g per day less than the *b* and *a* chicks respectively. At Walney these differences were 4.2 and 6g per day. Differences in skeletal growth followed the same pattern, the growth of T.H.B. per day being 0.15 and 0.18mm less than for *c* chicks than *b* and *a* chicks at Sanda and 0.19 and 0.22mm at Walney. Growth rates have been shown to correlate with a chick's likelihood of fledging (Hunt 1972). In spite of this, *c* chicks survived as well as *a* and *b* chicks at Walney, although not at Sanda.

Mortality of *a* and *b* chicks occurred earlier at Sanda than at Walney. In spite of this no difference in survival to fledging was found between colonies. This may be an artifact due solely to the differences between colonies in nesting substrates. In view of the difficulty in locating small (<3 week old) chicks At Sanda the gulls nest in boulder beaches, which provide lots of hiding places for chicks. At Walney chicks were far more easily located as they were usually found in the provided nest shelters or in the nearest rabbit burrow. As chicks grew at Sanda, their size prevented them from using all but a few hiding places. Chicks also tended to use the same places between visits so after they had been located for the first time after leaving the nest, they were more easily re-located on subsequent visits. Chick presence was therefore probably more accurately assessed for older rather

than younger chicks at Sanda. Apparent chick disappearance (taken as mortality) was therefore likely to be earlier at Sanda than at Walney. This would explain why in spite of apparent higher early mortality at Sanda, survival to 4 weeks post-hatch did not vary for *a* or *b* chicks between colonies.

Surprisingly few data are available on the fledging success at British Herring gull colonies. Published data are difficult to interpret as timing of fledging is not always defined (Graves *et al.* 1984), or methods of assessing fledging success are different, for example this study and Paynter (1949) calculate fledging success from the number of chicks that were known to survive to 4 weeks post-hatch (this study) or actual fledging (Paynter 1949). In contrast, Brown (1967) assessed fledging success by counting the number of marked chicks that survived to 10 days post-hatch and then subtracting the number of marked chicks that he found dead that had died before fledging. The former method probably underestimates fledging success, as chicks may not be found as they approach fledging. The latter method will undoubtedly over-estimate fledging success, as the remains of many chicks that do not fledge are never found (Harris 1964).

In this study survival was only measured to four weeks post-hatch thus arriving at an overestimate of fledging which normally occurs at about 35-40 days (Cramp and Simmons 1983). Mortality between four weeks post-hatch and fledging has been found to be less than 5% (Paynter 1949, Davis 1975), so this overestimate is likely to be small. The levels of survival to fledging were higher at Sanda and Walney than the levels found by Darling (1938) for the Summer Isles 1937-38, and Harris (1964) at Skomer in 1962, by 30% per chick and >0.7 chicks per brood respectively. The difference could be due to only nests where three chicks hatched being used in this study, if adults that hatched 3 chicks were of a higher average "quality" than those that did not. Data on this are however lacking.

The levels of fledging success at Sanda and Walney were similar to that found on Skomer by Davis (1975) and although success per brood was lower, survival per chick was similar.

This apparent difference is due to Davis measuring survival per brood from broods where not all eggs hatched. Brown (1967) found a higher level of chick survival than I found at either Sanda or Walney, however his estimate was arrived at in a very different way. He calculated fledging success by marking a sample of chicks and counting the number that survived to ten-days post hatch. He then estimated survival to fledging by subtracting the total number of marked chicks found dead from the total sample. This would undoubtedly overestimate the survival of the sample as only a small proportion of chicks that do not fledge are actually found dead (Harris 1964, *pers obs*) as many presumably leave the natal area before dying, or simply disappear. Another methodological difference that could inflate Brown's fledging success, was that he used chicks from various brood sizes. Chicks from broods of less than three would be individually more likely to survive to fledging than chicks from broods of three as they would experience less sibling rivalry (Harris 1964). This difference between survival of chicks from different brood sizes explains the difference between the survival rates per brood and per chick for Sanda (survival per chick was arrived at using chicks from all brood sizes, whereas survival per brood is calculated for broods of three).

The fledging success on the Isle of May for 1978-80 (Graves *et al.* 1984) was much higher than the findings for Sanda and Walney, presumably as the number of breeding pairs in the colony there had been massively reduced by culling. This reduced the competition for food between breeding birds, as reflected by the reduced age of first breeding and clutch volume found at that colony (Coulson *et al.* 1982), and probably resulted in the extremely high fledging successes.

The exceptionally high fledging successes found by Monaghan (1979) for two roof top nesting colonies of Herring gulls appeared to be due to reduced con-specific predation, although the possibility that increased access to food reserves was not ruled out (Monaghan 1979).

Number of breeding birds in third year plumage

While none were found breeding at Sanda, the proportion of breeding birds exhibiting characteristics of third year birds at Walney was extremely high. This would appear to reflect lower competition at Walney, as in the studies of Coulson *et al.* (1982) and Duncan (1978). The proportion of third year birds breeding at Walney was higher than on the Isle of May where the number of breeding pairs had been reduced by culling from 26,000 pairs in 1970, to <6000 pairs in 1981. The proportion was not higher than that found by Duncan at Mallowfield Fell. There is one important difference in the way that Duncan and Coulson collected their data to this study. The proportion of third year birds recorded in these studies represent the number poisoned in culls, not numbers observed breeding. On many occasions at Sanda and particularly Walney, I observed immature birds loafing around the colony, normally on the periphery of the colony but on many occasions in the centre as well. These birds were seen to feed opportunistically, klepto-parasitising adults and on occasion predating chicks or eggs. It seems likely that if poisoned bait was placed in a colony, that not only would breeding birds eat the bait, but that the immatures loafing around the colony would also be poisoned. This would result in the proportion of birds culled in third year plumage being higher than the proportion of breeding birds in third year plumage (unless a very large number of non-breeding adult plumaged gulls were also loafing around the colony which is extremely unlikely).

Effect of breeding success on population changes

Both Sanda and Walney enjoyed high levels of breeding success during the seasons of study. Breeding performance at Walney was higher than at most colonies studied previously in Britain. As these colonies were all increasing at the time of study, it seems unlikely that differences in breeding success between colonies could account for the observed changes in breeding populations. This of course assumes that the study at Walney was not carried out during an exceptionally good breeding season and that, in fact breeding failure is not normal at the colony. No other recent studies of breeding success

are available for Walney; however both the gull ringers and the warden felt that the breeding season in 1990 was fairly typical of recent years (T. Dean *pers comm*). Whilst this in itself is not sufficient evidence to rule out breeding failure having contributed to the recent decline in the number of breeding pairs at Walney, the other data presented in this chapter suggest that another factor was far more important. The large proportion of third year birds breeding at Walney and the large egg volumes recorded both match the findings of Coulson *et al.* (1982) and Duncan (1978), working at colonies where the number of breeding pairs had been massively reduced by culling. These results were interpreted in both studies as having been due to reduced competition between breeding birds. If this is true at Walney, then the reduced competition presumably also resulted in the observed increase in clutch size and hatching success at Walney since Brown's study in 1962-65, as no increases in food supply available to gulls at Walney appears to have occurred in the intervening years (see Chapter 3). It seems likely then, that the decline at Walney has occurred as a result of high adult and possibly immature mortality, rather than poor breeding success lowering recruitment.

CHAPTER 7

CRITICAL EVALUATION OF THEORIES REGARDING HATCHING ASYNCHRONY AND THE PREDICTIONS THEY MAKE ABOUT REPRODUCTIVE ORGANISATION IN THE HERRING GULL

INTRODUCTION

In most Larids that lay a clutch of more than one egg, the hatching of the young is not synchronous: successive eggs hatching several hours, or even days apart. Several studies have investigated the adaptive significance of this hatching asynchrony, the assumption being that this pattern has evolved as the optimum strategy by the parent to maximise reproductive success (Quinn and Morris 1986 - Caspian Tern (*Sterna caspia*), Parsons 1975, Graves *et al.* 1984, Parsons 1975, - Herring Gull (*Larus argentatus*)). The premise of all of these studies, that hatching asynchrony maximises the number of young reared, has not been conclusively demonstrated in gulls.

Two studies of the effect of different degrees of hatching asynchrony on breeding success have been made in an attempt to establish the adaptiveness of hatching asynchrony; Hahn (1981) on the Laughing Gull (*Larus atricapilla*), and Hébert and Barclay (1986) on Herring gulls. The results of these studies are ambiguous. Both studies investigated the significance of hatching asynchrony regardless of the possible adaptive function of the small *c* egg (Parsons 1970). In both studies, synchronous broods were created by taking three eggs laid on the same day from the same point in the laying order i.e. 3 *a* eggs or 3 *b* eggs etc. In the study by Hahn (1981), of 13 synchronous broods created, 8 comprised of *c* eggs only. Parsons (1970), demonstrated that *c* eggs produced chicks less likely to survive than did *a* and *b* eggs, partly as a result of their smaller size. This *c* chick disadvantage could therefore mask any result due to the differing degrees of hatching synchrony/asynchrony. Hébert and Barclay (1986), studied chick growth for the first 5 days post-hatch, and chick survival to forty days. However, their study was carried out in a year of poor breeding success (with only 11% of chicks from control nests, and 13% of chicks from synchronous nests surviving to fledging), and no difference was found in chick survival between the synchronous and the asynchronous groups. Differences between chick growth rates were found, with *a* chicks from asynchronous broods growing quicker than chicks from synchronous broods, but the smallest chicks growing quicker in the

synchronous broods than *c* chicks in asynchronous-hatching broods.

Several aspects of Larid breeding biology appear pertinent to any discussion of hatching asynchrony. However, these have seldom been discussed in this context. The aim of this section is to present information about these aspects, and use these, and what is known about hatching asynchrony in the Herring gull, to evaluate the current hypotheses regarding hatching asynchrony in birds and whether any of these hypotheses can explain the observed pattern of reproduction in the Herring gull. The aspects to be examined are; The degree of hatching asynchrony compared to the laying asynchrony, the delayed incubation of the first laid egg, the production of a smaller egg at the end of the laying sequence, the timing of chick mortality, and the truncated clutch size in the Herring gull.

Of the hypotheses regarding hatching asynchrony, several make very similar predictions, and are therefore difficult to separate experimentally. It is possible that different hypotheses may explain different aspects of hatching asynchrony in the Herring gull; however the aim of this section is to determine which, if any, of the hypotheses is likely to be the main cause of Herring gulls organising their reproductive output in the way they do. I will first present the hypotheses regarding hatching asynchrony and the general areas of Herring gull breeding biology of relevance to this discussion. Each hypothesis will then be discussed and assessed as to whether predictions they make match what is known about the Herring gull's breeding biology.

Unless otherwise stated, the discussion will be of reproductive organisation of three-egg clutches.

The current hypotheses are;

7.1.1 - Brood Reduction hypothesis

This hypothesis presented in Lack (1954), states "asynchronous hatching is a valuable adaptation because it results in the nestlings being of very different size, with the result

that, when food is short, as it often is, all of it goes to the larger chicks, while the younger chick or chicks quickly die". Lack proposed this hypothesis for species where food availability during the breeding season could not be predicted at the time of egg-laying. He argued that asynchronous hatching would result in a hierarchy forming within the brood, with older chicks being dominant. The brood size would be reduced to the optimal brood size, by smaller chicks being unable to compete with their larger siblings and consequently starving.

7.1.2 - Sibling Rivalry Reduction hypothesis

"Hatching asynchrony is an example of manipulation by the parents, who thereby impose a dominance hierarchy on the chicks and hence reduce energy wasted by the chicks in competing with each other" (Lessells and Avery 1989, Mock and Ploger 1987). This hypothesis is similar to the brood reduction hypothesis in that it explains the role of hatching asynchrony as being to create a hierarchy within the brood. Whereas the brood reduction hypothesis suggests that brood reduction acts to optimise brood size to environmental conditions by death of younger chicks, this hypothesis acts by reducing the amount of energy wasted by chicks competing with each other. This argument was used to explain hatching asynchrony in gulls by Hahn (1981).

7.1.3 - Nest Failure hypothesis

"Hatching asynchrony is a time-saving mechanism, reducing the time in which older chicks are vulnerable to predation" (Clark and Wilson 1981). In species where predation in the nest is high, parents should incubate eggs as soon as they are laid, thus decreasing the length of time that the first laid eggs and resultant chicks are present in the nest. This hypothesis was originally proposed to explain hatching asynchrony in species where predation is high in the nest (Clark and Wilson 1981). It could however still be true of semi-precocial species such as the Herring gull, where pre-fledging predation is high. Older chicks could avoid predation either by becoming larger quicker and thereby being less vulnerable to predators, or by fledging earlier than if hatching was synchronous.

7.1.4 - Hurry-up hypothesis

"Older chicks are able to fledge earlier than siblings, when feeding conditions are deteriorating at the end of the breeding season" (Hussell 1972). Like the nest failure hypothesis, this hypothesis is primarily concerned with hatching asynchrony being a result of incubation of eggs as soon as they are laid so that chicks fledge as soon as possible. This hypothesis was originally formulated regarding individuals breeding at the end of a breeding season, when feeding conditions are deteriorating, the advantage being that chicks fledging earlier could make the most of the limited food availability (Hussell 1972). This hypothesis only makes predictions about hatching asynchrony towards the end of the breeding season; however this need not be the case. In the Herring gull it could be that fledglings have a finite amount of time in which to acquire foraging skills through either learning, or development of physical skills (such as plunge-diving), before a time of food shortage (possibly late summer, the time when adult body weights are at their lowest). The longer a bird has to develop these skills, the higher it's chances of surviving the times of food shortage. It would then pay parents to incubate as soon as possible to maximise the amount of time each chick has to develop it's skills.

7.1.5 - Peak Demand hypothesis

This hypothesis argues that hatching asynchrony is an adaptive strategy in that "by staggering the hatching of chicks, the maximum daily feeding rate that the parents must achieve is lower" (Hussell 1972). The hypothesis argues that in species where food demand from individual chicks is high, then the adults may stagger the hatching of a brood. This results in the peak demand for each chick falling at a different time so that the maximum daily rate of provisioning that the adults must achieve is reduced.

7.1.6 - Insurance hypothesis

The idea of the insurance hypothesis is that "the last egg(s) in a clutch represent a hedge by the mother against other eggs in the clutch failing to hatch. Should all of the chicks

hatch, hatching asynchrony ensures that the supernumary chick quickly starves and does not threaten the growth or survival of the other chicks" (Lessells and Avery 1990). This hypothesis makes no predictions regarding the adaptive significance of hatching asynchrony (Nisbet 1973, Stinson 1979); however it has been used to explain the small size of the *c* egg in the Herring gull. Since Graves *et al.* (1984), argued that the supernumary chick would starve according to the brood reduction hypothesis, it is pertinent to discuss this hypothesis with regards to hatching asynchrony.

Aspects of the reproductive organisation of Herring gulls relevant to hypotheses regarding hatching asynchrony.

The degree of hatching asynchrony in the Herring gull

The Herring gull typically lays three eggs. These eggs are laid on alternate days leading to a laying span of five days (MacRoberts and MacRoberts 1972). By the time of hatching, this five day laying span is reduced to an average hatching span of less than two days (MacRoberts and MacRoberts 1972). Thus the spread of hatching is in fact more synchronous than the spread of laying. This increased hatching synchrony, in comparison to laying synchrony, is a result of two factors; firstly, the *a* egg is not fully incubated until the *b* egg is laid, resulting in delayed hatching of the *a* egg (MacRoberts and MacRoberts 1972). Secondly, the *c* egg is significantly smaller than either the *a* or *b* eggs, and consequently requires a shorter incubation period (Parsons 1972).

The timing of chick mortality

Peak chick mortality in Herring gulls occurs during the first week post-hatch (Paynter 1949, Harris 1964, Kadlec and Drury 1968, Parsons 1975). Weaver (cited in Kadlec *et al.* 1969), concluded that this high early mortality was a result of "the failure of adults to make an adequate behavioural transition from incubation to care of young". Harris (1964), similarly considered that chick mortality during the first week post-hatch must be due to inadequate parental brooding behaviour as "It appeared that none succumbed directly to

starvation. It seems unlikely that food shortage would affect very small chicks when adults were able to supply food for young approaching their own weight". The results of Parsons (1971) however suggest that this is not true, and that in fact the first week post-hatch is the only time when a chick's skeletal size and available reserves have a measurable effect on it's likelihood of fledging. He found that "the most important factor in determining post-hatching survival is the size of the egg", but that this only affected survival during the first week post-hatch. He also showed that increased egg size increased a chick's survival probability through the resultant increased skeletal size and yolk reserves. This finding, and the observed high chick mortality during the first week imply that this period is the most crucial in chick rearing in spite of it being the time of lowest daily energy requirement for chicks (Dunn 1976). Graves *et al.* (1984), tested the idea that early chick mortality could be due to starvation by providing supplementary food at nests with small chicks (<3 days old). They found that this extra food increased the rate of weight gain in chicks, increased fledging success, and increased the amount of time that both parents spent on territory. The amount of time both adults spent on territory did not correlate with the number of chicks dying in the first five days post-hatch so parental presence itself did not result in increased fledging success and rates of weight gain. Their results appear to demonstrate that in spite of the chick's small size and low energy requirements, chick growth and survival is food limited during the first week post-hatch. The reason for high chick mortality at a time when energy demand is low was, they concluded, a strategy employed by the parents to reduce their brood size through brood reduction "By hatching the three eggs but setting the foraging effort low initially, the parent is more likely to rear a brood of two, which may be optimal".

The truncated clutch size in the Herring gull

Herring gulls mostly lay three eggs (>65%), two egg clutches are less common (<30%), one egg clutches uncommon (<7%), and four egg clutches rare (<0.5%) (Harris 1964, Brown 1967, this study). Most authors now agree that clutch size is controlled at the number that will maximise the lifetime reproductive success (L.R.S.) of a female.

Differences in individual quality (as measured by L.R.S.) have been demonstrated in a wide range of species (see Newton 1989 for a wide range of studies), including the larids Kittiwake (*Rissa tridactyla*) (Coulson and Thomas 1985) and Red-billed Gull (*Larus novaehollandiae scopulinus*) (Mills 1989). In view of these findings, one might expect optimal clutch size for each female to vary more widely then is observed in larids, with in particular more larger clutches being laid.

Clutch size appears to be limited to three not only in the Herring gull, but in all large gulls studies (e.g. Lesser Black-backed gull, *Larus fuscus* (Harris and Plumb 1965), Western gull, *Larus occidentalis*, (Pierotti and Bellrose 1986), Ring-billed gull, *Larus delawarensis*, (Meathrel and Ryder 1987). Experiments to test whether a clutch size of three is optimal in these species have been made by measuring fledging success and chick growth rates for chicks from experimentally enlarged broods. Results have varied between studies; In the Herring gull Spaans (1971) and Harris and Plumb (1965) failed to find differences in breeding success with increased brood sizes; however in the case of Harris and Plumb (1965), this was due to adverse weather resulting in the deaths of most study chicks. Haymes and Morris (1977) found that Herring gulls were able to raise broods of more than four young. Three other species have also been shown to be capable of rearing broods of more than three; Glaucous-winged gull (*Larus glaucescens*, Vermeer 1963, Ward 1973), Lesser Black-backed gull (Harris and Plumb 1965) and Western gull (Coulter 1973). Fledging success alone may not indicate increased breeding success, if enlarged broods fledge underweight chicks with lowered survival probabilities than chicks from normal sized broods. The results of comparing fledging weights of chicks from normal and enlarged broods have revealed conflicting results. Haymes and Morris (1977) found no difference in the fledging weights of chicks from control broods and artificially enlarged broods with up to five chicks. In the Glaucous-winged gull, Ward (1973) found no difference in fledging weights in broods of 1-6 chicks at one study site, but found a decline in fledging weight with brood size at another site. Reid (1988), found that fledging weight and wing length decreased with increased brood size, while incubation length increased.

Coulter (1973) found a decline in the individual fledging weights of chicks with increased brood size (up to six chicks) in the Western gull. Only two attempts have been made to investigate post-fledging survival for chicks from enlarged broods, and these appear to suggest that experimentally enlarged broods are more productive than normal broods. Vermeer (1963), found that post-fledging survival of chicks from artificially enlarged broods was higher than that of chicks in control broods, based on off-colony sightings. Ward (1973) in three studies, found that in two years (in two different colonies) broods of six chicks had the highest number of chicks surviving after fledging and, in one year, broods of three had the highest success.

The results of these studies indicate that while in some years the modal clutch size of three is optimal in terms of chick productivity, in other years, chick productivity could be increased if clutch size was increased. These studies do not take into account the effect of rearing enlarged broods on adult survival. Increased parental investment may increase fledging success per bout at a cost to adult survival and thus not in the long run be a sound strategy for adult gulls. It would seem more likely however that adult gulls should reduce their investment if their survival is threatened by low body reserves, and that any "strain" would result in starvation of chicks, not reduced survival of adults. This has been suggested to be the case in Arctic Terns (Monaghan *et al.* 1989).

Brood enlargement experiments on Larids have all neglected to control for the effects of having to produce the fourth egg (Bolton 1991), enlarged broods having been created by the addition of an extra egg or chick from another pair. They have also assumed that incubating adults can incubate clutches of more than three eggs. Bolton (1991), investigated these two problems experimentally in the Lesser Black-backed gull. He increased clutch size by removing the *a* egg as soon as it was laid so that the female continued laying until three eggs were in the nest. He then replaced the *a* egg to form a clutch of four eggs. In another group of nests he simply placed a fourth egg into a newly completed clutch of three. He found that clutches of four hatched significantly more eggs

than did clutches of three and thereby dismissed the argument that clutch size is limited by the incubation capacity of the parents. He also found no difference in hatching success or number of chicks reared per brood, between those nests with an additional fourth egg and those that had been induced to lay four eggs by the removal of the *a* egg. It appears therefore that the costs of producing a fourth egg had no effect on breeding success in enlarged broods.

The clutch size of gulls appears then to be limited to three, a clutch size smaller than that which would produce the maximum number of chicks per breeding bout.

INDIVIDUAL DISCUSSIONS

Brood Reduction hypothesis

The decrease in hatching asynchrony over laying asynchrony does not seem consistent with this hypothesis, as the two ways in which this decrease is produced both have costs in terms of chick productivity; Firstly, the delayed incubation of the *a* egg means this egg is at an increased risk of predation as a result of being in the nest longer than if it was incubated as soon as it was laid. Secondly, the small size of the *c* egg reduces the likelihood of the resultant chick fledging, as the *c* chick hatches with lower protein reserves and is skeletally smaller than it's siblings. As a result it is less able to compete.

The brood reduction hypothesis predicts that clutch size should be optimal in years of high food availability, but larger than optimal in poorer years. The results of brood enlargement experiments show that this clearly is not the case, with optimal brood size being 3 in some years but considerably higher in others.

Sibling Rivalry Reduction hypothesis

This hypothesis can be rejected on the same grounds as the brood reduction hypothesis.

Nest Failure hypothesis

This hypothesis has been argued convincingly for a wide range of species (see Clark and Wilson 1981 for a review); however for the Herring gull it does not match the observed pattern of hatching asynchrony. The most obvious objection is that if the main factor affecting chick survival is pre-fledging predation, then the *a* egg should be incubated as soon as it is laid. This is not the case. Unlike most of the species in Clark and Wilson (1981), Herring gull chicks leave the nest shortly after hatching, and nest predation is comparatively low. Predation of chicks prior to fledging may be high and result in early-fledging chicks being at an advantage. It is difficult however to assess to what extent chick predation is related to food availability for several reasons: predation may be a result of adults spending more time foraging off territory in times of poor food availability. Secondly, starving chicks tend to be more active and may wander into neighbouring territories where adults attack them. The actual measurement of predation level is also difficult. Most studies regard chicks that have disappeared from territories as having been predated. This need not be true if starving chicks have strayed off territory. Territories are also flexible, so disappearance of broods may be a result of territorial shift (possibly as a result of observer disturbance), or the inability of the recorder to find them, not necessarily predation.

If nest predation was the main factor controlling breeding success, then the amount of time spent in the nest should be minimised. To achieve this, Herring gulls should lay the smallest viable eggs to reduce incubation time. Manipulations of hatching order have shown that *c* chicks are only at a slight disadvantage to *a* and *b* chicks as a result of lowered egg reserves, and that hatching order itself is the main case of higher mortality in *c* chicks (Parsons 1970). If nest failure hypothesis did account for hatching asynchrony in the Herring gull, then it would seem likely that female gulls would lay three *c* eggs. This is not the case.

Predictions made by the nest-failure hypothesis do not match what is known of Herring gull breeding biology. The delayed incubation of the *a* egg and the large sizes of the *a* and *b* eggs are not in accordance with the hypothesis, so this hypothesis may be rejected as an explanation for hatching asynchrony in the Herring gull.

Hurry-up hypothesis

This hypothesis makes identical predictions to the nest failure hypothesis with regards to hatching asynchrony and can be dismissed for the same reasons.

Peak Demand hypothesis

The peak demand hypothesis argues that hatching asynchrony is advantageous. It does not then explain why hatching asynchrony is reduced from the degree of laying asynchrony at a cost to the survival of the *a* and *c* chicks (see brood reduction hypothesis discussion), nor does it explain the small size of the *c* egg. It also seems unlikely in the Herring gull as hatching asynchrony is reduced to 2 days. Thus, for a brood of three chicks, peak demand would fall for two chicks on the same day, and for the other chick on a consecutive day. Peak energetic demand in Herring gull chicks is reached at around 36 days post-hatch (Dunn 1976) and remains at the same level until at least 50 days post-hatch. The "peak" lasts much longer than the time between chicks hatching so this hypothesis is inappropriate.

The timing of chick mortality suggests that the time of peak energy demand in Herring gull chicks is of little consequence in terms of survival, as chick mortality after the first week post-hatch is comparatively low (e.g. Paynter 1949, Kadlec *et al.* 1968). By far the highest mortality occurs when the chicks are less than one week old, when energy demands are at their lowest (Dunn 1976).

This hypothesis offers no explanation as to why Herring gull clutch size is limited at three eggs.

Insurance hypothesis

The insurance hypothesis offers no explanation as to why incubation of the *a* egg is delayed; however it may explain the small size of the *c* egg and the truncated clutch size. The hypothesis predicts that when the *a* and *b* chicks hatch, the *c* egg or chick should not survive, and this could explain why chick mortality is high in the first week post-hatch. *C* chick mortality is higher than in the *a* or *b* chicks in the first week post-hatch (Parsons 1970); however, the pattern of mortality does not match that predicted by the insurance hypothesis. Firstly broods of three are not reduced to broods of two. Most studies where breeding success is moderately high report a larger number of nests fledging three chicks than one might expect if the insurance hypothesis was true (e.g. Graves *et al.* 1984 found that 8% of nests where all three chicks hatched went on to fledge three chicks). Thus it appears that breeding gulls are certainly capable of rearing at least three young, so the small size of the *c* egg cannot be explained by the insurance hypothesis. Experiments showing that experimentally enlarged broods are more productive than natural broods of three, further support this objection.

The insurance hypothesis does not explain any aspects of the Herring gulls breeding biology, and the prediction that brood size should be reduced if all three chicks hatch is not what is observed. The insurance hypothesis may therefore be rejected.

GENERAL DISCUSSION

The delayed incubation of the *a* egg and the small size of the *c* egg cannot be explained by any of the hypotheses discussed. The pattern of reproductive organisation in the Herring gull may be better explained by looking at the spread of hatching in terms of synchronisation rather than asynchrony. The decreased survival probability of the *a* (as a result of delayed incubation) and *c* (as a result of it's small size) can only be explained if

the small size of the *c* and the delayed incubation of the *a* result in some advantage by increasing synchrony. If synchrony is beneficial, then this could also explain the truncated clutch size. To increase the clutch size without lengthening the hatching span would require either delaying incubation of the two first laid eggs (*a* and *b*, by four and two days respectively), or by further reducing the size of the last laid (*d*) egg.

The reason for gulls not delaying incubation further could be due to resultant increased predation of the first laid egg/s, or of delayed incubation leading to reduced egg viability (as measured by hatching success or chick survival). Hen's eggs stored for the full incubation period at low temperatures (26 to 35°C) suffer lower hatching success than those stored at (35 to 40.5°C). The embryos in the eggs stored at lower temperatures also suffer disproportionate development, absence of organs and malformations (Lundy 1969). The effect of low temperature on hatching success was also found to be greater during the first 16 days of incubation than later (Lundy 1969). In Larids, Reid (1987) tested the effect of delayed incubation on hatching success in the Glaucous-winged gull. He found a slight decline in hatching success in eggs not incubated immediately, although this trend was not significant. His experimental design would however, have required hatching success to below 68% before it would be significantly different from his control group (control n=21, hatching success = 95%, experimental n=20).

The reduction in the size of the *c* egg in three egg clutches is large enough to affect the survival probability of the resultant chick as a result of the small skeletal size and low levels of protein reserves this leads to (1972). According to Parsons, the reduction in egg volume required for a fourth egg to hatch on the same day as the *c* (assuming it was laid two days later), would be 20g (using his egg size data against figure 1 pg 537). In his study this would have resulted in a *d* egg of only 49.5 - 50.5g. Parsons (1972), found that "nearly all the chicks from eggs smaller than 65 cm^3 died soon after hatching", so this reduction in size would result in a chick so small and poorly provisioned that it would probably not be viable.

The occurrence of peak chick mortality at a time when energy demands are at their lowest would appear to support the arguments of Harris (1964) and Weaver (cited in Kadlec *et al.* 1969), that this mortality is a result of inadequate parental care . Their argument is based on the argument that "it seems unlikely that food shortage would affect very small chicks when adults were able to supply food to young approaching their own weight". This assumes that food is as available to foraging parents when the chicks are small as when they are at their peak energy demand. No information is available to support or negate this assumption. It also assumes that the composition of the chick diet remains the same throughout the chick rearing period. This has been found not to be the case.

Gull chicks are fed a different diet than that which adults feed on during incubation (Annett 1989). This switch in prey types is not due to a seasonal change in the availability of different prey types, as late nesters and experimentally delayed nesters do not switch prey types until their eggs hatch (Pierotti and Annett 1986, Annett 1987). Chick diet also changes at around 5-7 days post-hatch (Pierotti and Annett 1986, this study). The period leading up to this second change coincides with the period of high mortality. If this mortality is due to the chicks requiring a special diet during the first week post-hatch, then this could offer an explanation as to why synchronous hatching could be advantageous in the Herring gull. This would require the following conditions to be true;

1 - Mortality is controlled by availability of food suitable for chicks less than 1 week post-hatch ("babyfood"). The finding of Graves *et al.* (1984), that provisioning small chicks with supplementary food (200g of KiteKat cat food per nest per day until the *a* chick was 5 days old) leads to increased fledging success 5 weeks later suggests that this condition is true.

2 - The babyfood offers a lower return in terms of energy delivery per unit time (or some other nutrient controlling chick growth/mortality), than the prey which is fed to the chicks older than 1 week post-hatch ("gross prey"). No evidence is available to support or negate

older than 1 week post-hatch ("gross prey"). No evidence is available to support or negate this condition, although prey fed to larger chicks is often larger than that fed to chicks less than 1 week old (Pierotti and Annett 1986, *pers obs*). This allows adults with larger chicks to exploit a wider range of preys than those with small chicks. I have observed broods of young chicks that have apparently died of starvation, that have been surrounded by food that was too large for them to ingest (*Carcinus maenas*).

3 - That the switch from babyfood to "gross prey" is controlled by chick age and not prey availability. Pierotti and Annett (1986) and the findings of my diet studies on both Sanda and Walney (Chapter 3) suggest that this is the case.

In this scenario, the time spent feeding on the babyfood would be minimised by synchronous hatching, as the period in which at least one chick in the nest required babyfood would be one week (the age at which the prey change occurs). If hatching asynchrony was equal to laying asynchrony, then the period in which at least one chick was less than 1 week old would be equal to the seven days + the hatching span (7 + 5 = 12 days).

Parents would have three options in terms of prey choice;

1 - Provision the chicks with both prey types. This would require foraging on an "expensive" (babyfood) and a "cheap" (gross prey) food supply, thus reducing gross energy intake (as a result of the high cost of the babyfood and possibly having to forage in different areas or use different techniques to collect the two prey types). As the order with which the chicks are fed is dependent on the arrival order of the chicks at the regurgitating parent (Graves *et al.* 1984) it seems unlikely that the parents could selectively feed the youngest/younger chick/chicks on the expensive prey. This is because the older chicks would arrive before the less dominant younger chick, and the younger chick would not receive most of it's food until the older chicks had fed. To ensure that the youngest chick received babyfood, the adults would have to feed the whole brood on babyfood, or

somehow regulate the distribution of different prey types to different members of the brood. There is no evidence that gulls are capable of the latter.

2 - Feed only on the "expensive babyfood" (E.B.), until the youngest chick is old enough to switch to the "gross" diet. This would lead to the older chicks achieving a lower rate of energy intake/time (the prey type received would be energy rich, but supplied in small quantities), but would result in the youngest chick being fed the appropriate diet. Foraging costs for the adults would increase for two reasons; firstly, the time spent feeding the older chicks on E.B. would be extended. Secondly, the older chicks would be feeding on E.B. as they grew and their energy demands became higher than in the first week post-hatch.

3 - Switch to the "gross prey" when the *a* and *b* chicks were old enough. This would result in the *c* chick receiving an inappropriate diet. The effect of this is not known; however the fact that gulls do feed their chicks on a special diet during the first week post-hatch (Pierotti and Annet 1986, Chapter 3) suggests that this would result in some disadvantage.

If adults were constrained in time that they could switch from expensive babyfood to "gross" prey by the age of the youngest chick, then the difference in babyfood requirements would be much larger. This can be seen from plotting the energy requirements of broods with different degrees of hatching asynchrony. In Figures 7.1 to 7.3, I have plotted the energy requirements of broods that hatch synchronously, broods that hatch with the "normal" degree of asynchrony (hatch span = 2 days) and broods where hatching asynchrony is equivalent to laying asynchrony (hatch on alternate days). The energy requirements are taken from Figure 2 in Dunn (1976). Figure 7.1 shows the energy requirements of a synchronously hatching brood of three, until the youngest chick is 1 week old (6 days post-hatch), the length of time the parents would have to spend provisioning the brood with E.B. would be 7 days, and the peak daily requirement would be 93 Kcal. In the normal asynchrony group (Figure 7.2), the parents would have to

supply E.B. for 9 days, with a peak daily requirement of 108 Kcal, and if hatching asynchrony was the same as laying asynchrony (Figure 7.3), then the figures would be 11 days and 131 Kcal respectively. The disadvantages of asynchronous hatching in this situation are an extended period of provisioning E.B., and an increase in maximum daily energy requirement from E.B. of 13.9% for normal hatching asynchrony, and 29.0% if hatching asynchrony was equal to laying asynchrony.

This hypothesis (the "Expensive Babyfood Hypothesis" hereafter referred to as the E.B.H.), appears consistent with the observations of various aspects of Herring gull breeding biology that no other hypothesis can explain; the delayed incubation of the *a* egg, the small size of the *c* egg, the truncated clutch size, and the high mortality when chicks are small and require comparatively little provisioning.

One observation of Herring gull breeding biology that does not appear to be consistent with the E.B.H., is that their clutches do not, as predicted, hatch totally synchronously. Several other groups of birds are capable of achieving remarkable degrees of synchrony e.g. the Greater Rhea *Rhea americanus*, a species where the male incubates and the female continues to add eggs to the clutch after incubation has commenced. The laying span of 9-12 days is reduced to a hatching span of 2-3 hours over an incubation period of 24-41 days (Faust 1960). This increased synchrony can be achieved either through delaying incubation until the clutch is complete (e.g. Skylark *Alauda arvensis* Delius 1963), or through chicks communicating by calls to synchronise their hatch time (e.g. Quail *Coturnix coturnix* see Vince 1970 for details and review).

For the E.B.H. to be correct, the degree of hatching synchrony must be constrained (as synchrony occurs only rarely in Herring gulls). This would presumably be as a result of delayed incubation resulting in lowered hatching success through either increased predation or of failure of eggs to hatch. The effect of delayed incubation on hatching success, and thus as a constraint on the degree of hatching synchrony that Herring gulls

can achieve, will be investigated in chapter 8.

Conclusions

The assumption that hatching asynchrony in gulls is adaptive has not been confirmed experimentally. No single hypothesis that could explain the adaptive nature of hatching asynchrony matches the observed pattern of reproductive organisation in the Herring gull. The hypothesis that increased hatching synchrony would be advantageous matches the observed pattern of reproductive organisation, and the dietary requirements of small chicks offers an explanation as to why Herring gulls show adaptations to reduce hatching asynchrony . The "expensive babyfood hypothesis" predicts that Herring gulls should maximise hatching synchrony, however this is not the case. The effect of delayed incubation on hatching success, as a possible constraint on gull's achieving hatching synchrony, will be investigated in chapter 8.

CHAPTER 8

EXPERIMENTAL EVALUATION OF THE "EXPENSIVE BABYFOOD HYPOTHESIS".

INTRODUCTION

In Chapter 8, the current theories regarding the adaptive significance of asynchronous hatching in birds were shown to make several predictions that run contrary to what is known about the reproductive biology of gulls. In view of the way that gulls organise their reproductive effort, I suggest that hatching asynchrony is not in itself adaptive, and that Herring gulls attempt to synchronise hatching to decrease the amount of time that a chick of less than 1 week old is present in the nest. This would minimise both the total amount of "Expensive Babyfood" needed to feed the brood, and the period of time over which this prey would be required.

In this chapter I experimentally tested several of the key predictions made by the Expensive Babyfood hypothesis and by conventional theories regarding hatching asynchrony, in an attempt to test these hypotheses. These experiments were as follows;

The effect of hatching synchrony and asynchrony on chick survival and growth.

Of the hypotheses regarding hatching asynchrony, all predict that hatching asynchrony is in itself a strategy employed by the female to maximise reproductive output. The E.B.H. however, exclusively predicts that hatching synchrony should maximise reproductive output, and that the observed pattern of hatching asynchrony is a result of constraints on the parents' ability to achieve full hatching synchrony. This prediction was tested by creating synchronously hatching broods and comparing these with a control group of unmanipulated asynchronous hatching broods.

The effect of delayed incubation on the hatching success of a eggs.

One way in which birds can achieve full hatching synchrony in a brood is to delay incubation of the clutch until the last egg is laid (e.g. Skylark *Alauda arvensis* Delius 1963). In Herring gulls, full incubation of the clutch does not commence until the *b* egg is laid

(MacRoberts and MacRoberts 1972) or until the full clutch is laid (Tinbergen 1971). Partial incubation of the *a* egg does however take place as soon as it is laid, resulting in the embryo commencing development. This development is on average, the equivalent to twelve hours development during full incubation, and thus contributes to the hatching asynchrony observed (Parsons 1972). A likely cause of this partial incubation is to keep the egg above ambient temperature, as low temperatures can have deleterious effects on both hatching success and embryonic development (Lundy 1969). The reason Herring gulls partially incubate the *a* egg could be that although this results in a disadvantage to chick survival through causing hatching to be asynchronous, it is necessary to ensure that the *a* egg remains viable. To investigate whether this was the case, the effect on hatching success was investigated by comparing eggs partially incubated with a sample of eggs not incubated until the second egg was laid.

The effect of supplementary feeding during the first week post-hatch, on chick survival and growth.

A key prediction of the E.B.H., is that the most important time for chick survival is during the first week post-hatch, when the chicks must be fed a special diet. High chick mortality at this time would appear to support this prediction; however several authors have suggested that this high mortality is due to parent gulls' inabilities to change from incubating to brooding behaviour (e.g. Weaver cited in Kadlec *et al.* 1969), or due to chicks dying through exposure (e.g. Harris 1964). By provisioning a sample of nests with extra food during the first week post-hatch, the importance of prey at this time and its effect on adult attendance and chick growth could be established.

The effect of brood age on adult attendance.

Several authors have pointed to the fact that chick energy demand is at its lowest during the first week post-hatch, and have thus assumed that breeding success could not be food limited at this stage. The E.B.H. however predicts that the specialist prey fed to chicks during the first week post-hatch, requires a higher foraging effort than prey fed to older

chicks whose energy requirements are higher. To investigate the foraging effort of parent gulls, the number of adults present on territory was recorded for broods from 1-4 weeks post-hatch (during the first week post-hatch chick, energy demands are at their lowest. By 4 weeks post-hatch, chicks are close to their maximum energy demands (Dunn 1976)).

METHODS

Induction of synchronous hatching

Nests were visited daily towards the end of incubation, when pipping eggs were recorded. Synchronous hatching (hatching span <24 hours) was induced by taking pipping *b* and *c* eggs and swapping these with the *b* and *c* eggs in a nest with a pipping *a* egg. Nests were checked after manipulation to ensure that chicks hatched synchronously (hatching span <24 hours); nests where chicks did not hatch synchronously were not included in the study. 20 clutches were successfully manipulated in this way. Control nests (n=42) were unmanipulated and hatching date for each egg and hatching span for the clutch were recorded. Hatching order for *a* and *b* chicks from synchronous hatching broods could not be ascertained so these were combined for comparisons with the control chicks. *C* chicks could be identified by their smaller size reliably, as in synchronous nests the *c* egg was always smaller than the *a* and *b* eggs. Mean Total clutch volume did not differ between control and synchronous-hatching broods (t_{60}=0.88).

Effect of delayed incubation on hatching success

A group of nests were visited daily so that laying day of the first laid egg could be accurately determined. When a new *a* egg was found, it was replaced with an artificial egg (made from Plaster of Paris, painted with acrylic paint and coated in all weather varnish) and removed. The collected eggs were stored loosely wrapped in tissue paper inside an open-topped metal tin, which was left in an elevated, well aerated hide situated in the gullery so that eggs experienced the ambient temperatures they would experience if they were not incubated. Eggs were not exposed to direct insolation; however this is unlikely to occur in "the wild", as adults often shade their eggs in strong sunlight (*pers obs.*). Eggs

were replaced in their respective nests after 48 hours by which time most nests possessed a second egg. The nests were then left until the eggs were due to hatch. At this time, nests were visited on alternate days and the hatching success of the different eggs recorded.

To avoid any biases introduced through the manipulation procedure (such as adults reducing incubation effort as a result of a strange egg being present in the nest), *b* and *c* eggs from the manipulated nests were used as the control group for comparisons of hatching success, as any reduced effort by the parents would affect these eggs as much as the *a* egg.

Supplementary feeding experiment - effect on chick survival and growth

Nests were visited daily to accurately establish hatching date of the first chick. After the first chick had hatched, supplementary food was placed on territory every evening until the oldest chick was 1 week old. The supplement used was 200g/day of Kit-e-kat catfood (following Graves *et al.* 1984) which was placed in the chick shelter by each nest to avoid stealing by neighbouring adults. Observations after feeding showed that the parent birds ate the supplementary food at each nest provisioned, normally as soon as they settled again after my visits. At several nests adults were seen to regurgitate the food to their brood, and although this was not confirmed at every nest, it is assumed that supplementary food was passed on to the chicks. 21 nests were provisioned with supplementary food; however in 2 of these, the full brood of 3 did not hatch so these were not included in the analysis.

Supplementary feeding experiment - observations of adult attendance

Observations of adult attendance at supplementary fed and control nests were made until chicks were four weeks post-hatch. During these watches, the number of adults within 5 adult body-lengths of any chick in the brood was recorded every 10 minutes. During the first 2 weeks post-hatch, chicks spent most of their time in the chicks shelters I had provided. As these were positioned next to nests, adults within 5 body-lengths were

probably the territorial parents, as Herring Gulls are intensely territorial with the territory being positioned around the nest site (Tinbergen 1953). When the chicks were older than 2 weeks post-hatch, the number of adults within 10 body-lengths was recorded, as the persistent begging by chicks older than this often drove adults further from the brood. Casual observation between the 10 minute scan samples supported the idea that birds within 10 body-lengths of the brood were in fact the respective parents, as these adults were seen to both feed the chicks, and defend them if non-parental adults approached within 10 body-lengths.

Observations were made for both control and supplementary fed nests at the same time to avoid biases due to different attendance at different times of the day. As the main aim of the experiment was to investigate the effect of supplementary feeding on chick survival, brood sizes were not held constant throughout the period of observation. To minimise the effect of brood size differences in adult attendance between the groups, only broods with >2 chicks were used in comparisons for the first 2 weeks, and broods with at least 1 chick for comparisons in weeks 3 and 4. Whilst this was not ideal, restricting analysis to larger brood sizes would have reduced the control sample to too few nests for meaningful comparisons to be made.

Effect of brood age on adult attendance

To investigate the way in which adult attendance varied by week until the chicks were four weeks post-hatch, only attendance at nests where at least 2 chicks survived to four weeks were used. This analysis did not include attendance of adults at supplementary fed nests during the period of food provisioning. As a large number of nests were excluded from this analysis, the coverage of observations in terms of time of day were not equal. To avoid any biases as a result of this, observations were split into four periods (05.00 to 09.59 hrs., 10.00 to 13.59 hrs., 14.00 to 17.59 hrs. and 18.00 to 22.59 hrs.) and comparisons for each time period made. Comparisons were made using X^2 tests to compare the proportion of observations in which two adults were present with the brood, and

observations where no adults were present. These measures were chosen as high attendance of two adults has been demonstrated to reflect periods when adults have low foraging costs (i.e. spend comparatively little time foraging, Graves *et al.* 1984), and absence of adults reflect periods when parents have high foraging costs (i.e. spend a lot of time foraging, Hunt and Hunt 1972).

RESULTS

Effect of synchronous hatching within a brood on chick survival and growth.

Synchronously hatching broods fledged proportionally more *a* chicks and *b* chicks than did control broods (Table 8.1), however no difference was observed for *c* chicks. Fledging success per brood was also higher for synchronous hatching broods than for control broods (Table 8.1). This was due to improved survival throughout the chick-rearing period, as no difference was found between chicks in timing of mortality (Figure 8.1).

Within treatments, hatching order had no effect on chick survival (Control - X^2=0.233, 2 d.f., P>0.05, Sync. - *a* + *b* versus *c*, X^2 with Yates' correction = 1.419, 1 d.f., P>0.05 Table 8.1).

Details of the growth rate analysis are presented in Table 8.2 and Figure 8.2. *A* and *b* chicks from control broods showed no difference in growth rate of T.H.B. from the combined *a* and *b* chicks from synchronous broods (*a* - $F_{1,163}$=0.72, N.S. *b* - $F_{1,163}$=3.41, N.S.). *A* chicks from control broods gained weight at a similar rate to combined *a* and *b* chicks from synchronous broods ($F_{1,163}$=0.31, N.S.); however control *b* chicks gained weight at a slower rate ($F_{1,163}$=6.68, P<0.05). *C* chicks from synchronous broods showed a higher growth rate for T.H.B. and a higher rate of weight gain than did control *c* chicks (T.H.B., $F_{1,134}$=9.89, P<0.01. Weight, $F_{1,134}$=7.41, P<0.01).

Within treatments, no differences were found between *a* and *b* chicks from control nests (Control - T.H.B., $F_{1,158}$=0.72, N.S. Weight, $F_{1,158}$=2.29, N.S.). Control *c* chicks grew slower than *a* chicks (T.H.B., $F_{1,162}$=8.97, P<0.01. Weight, $F_{1,162}$=24.14, P<0.001) and *b* chicks (T.H.B., $F_{1,162}$=7.10, P<0.001. Weight, $F_{1,162}$=16.91, P<0.001. There was no difference in growth of T.H.B. between *c* chicks and combined *a* and *b* chicks from synchronous broods ($F=_{1,136}$<0.01, N.S.); however *c* chicks gained weight slower than

Table 8.1 Cumulative mortality of chicks from experimentally manipulated synchronous hatching broods of three, and unmanipulated asynchronous hatching broods of three, during the first four weeks post-hatch, Walney 1990.

Colony	Chick	n=	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
Control	A	42	5 (11.9)	18 (42.9)	22 (52.4)	29 (69.0)
	B	42	17 (40.5)	23 (54.8)	25 (59.5)	31 (73.8)
	C	42	16 (38.1)	23 (54.8)	27 (64.3)	30 (71.4)
	Mean Brood Size	42	2.10	1.48	1.24	0.88
Sync. hatching	A+B	40	5 (12.5)	6 (15.5)	8 (20.0)	16 (40.8)
	C	20	3 (15.0)	6 (30.0)	10 (50.0)	12 (60.0)
	Mean Brood Size	20	2.60	2.40	2.10	1.60

Comparison of survival to 4 weeks post-hatch between groups;
Control a with Sync a and b - X^2 with Yates' correction=5.96, 1 d.f., $P<0.05$.
Control b with Sync a and b - X^2 with Yates' correction=8.25, 1 d.f., $P<0.01$.
Control c with Sync c - X^2 with Yates' correction=0.37, 1 d.f., N.S.

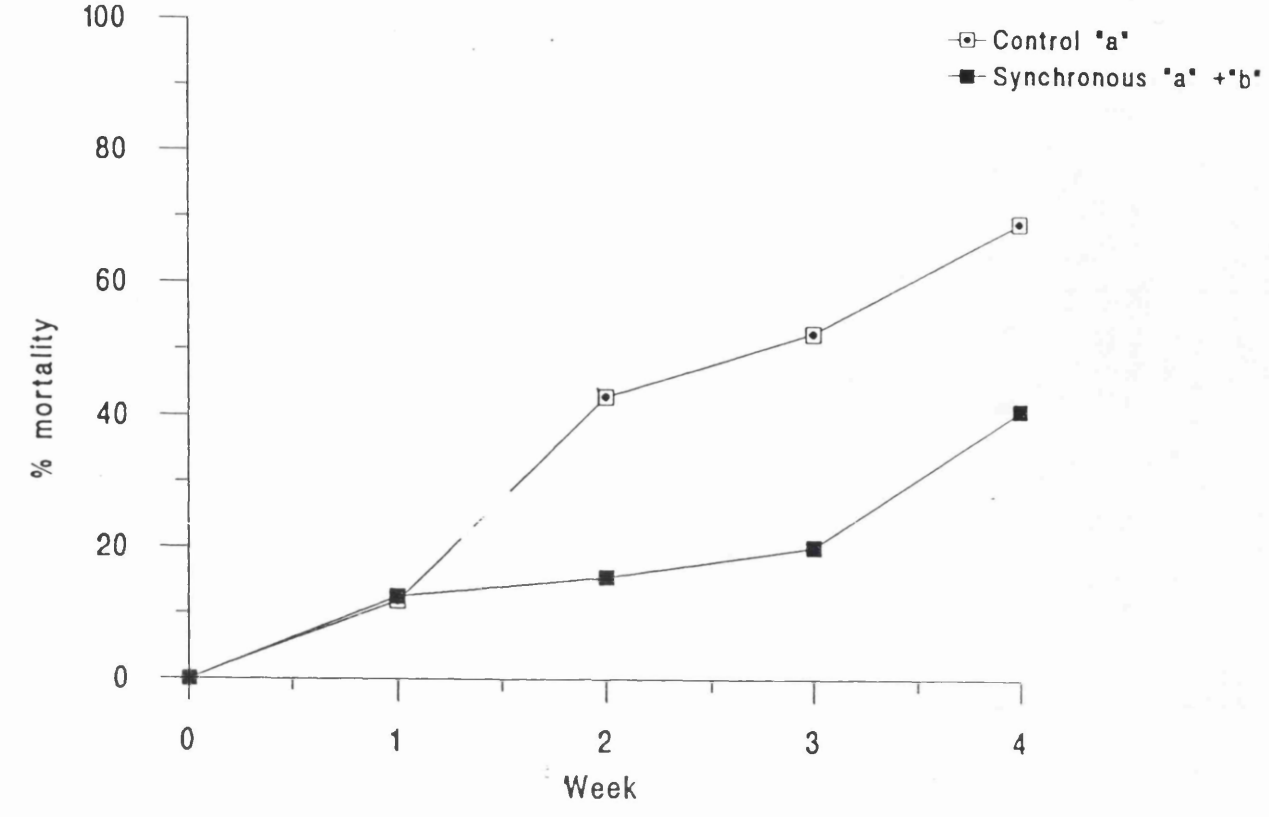
Comparison of survival per brood to 4 weeks post-hatch between groups;
Mann-Whitney U=278, $n_1=42$, $n_2=20$, $P<0.05$.

Figure 8.1a Cumulative mortality to 4 weeks post-hatch of "a" chicks from control broods and combined "a" and "b" chicks from synchronous-hatching broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=0.85, N.S.).

Figure 8.1b Cumulative mortality to 4 weeks post-hatch of "b" chicks from control broods and combined "a" and "b" chicks from synchronous-hatching broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=0.93, N.S.).


100
80
60
40
20
0
% mortality
0
1
2
3
4
Week
Control "a"
Synchronous "a" +"b"

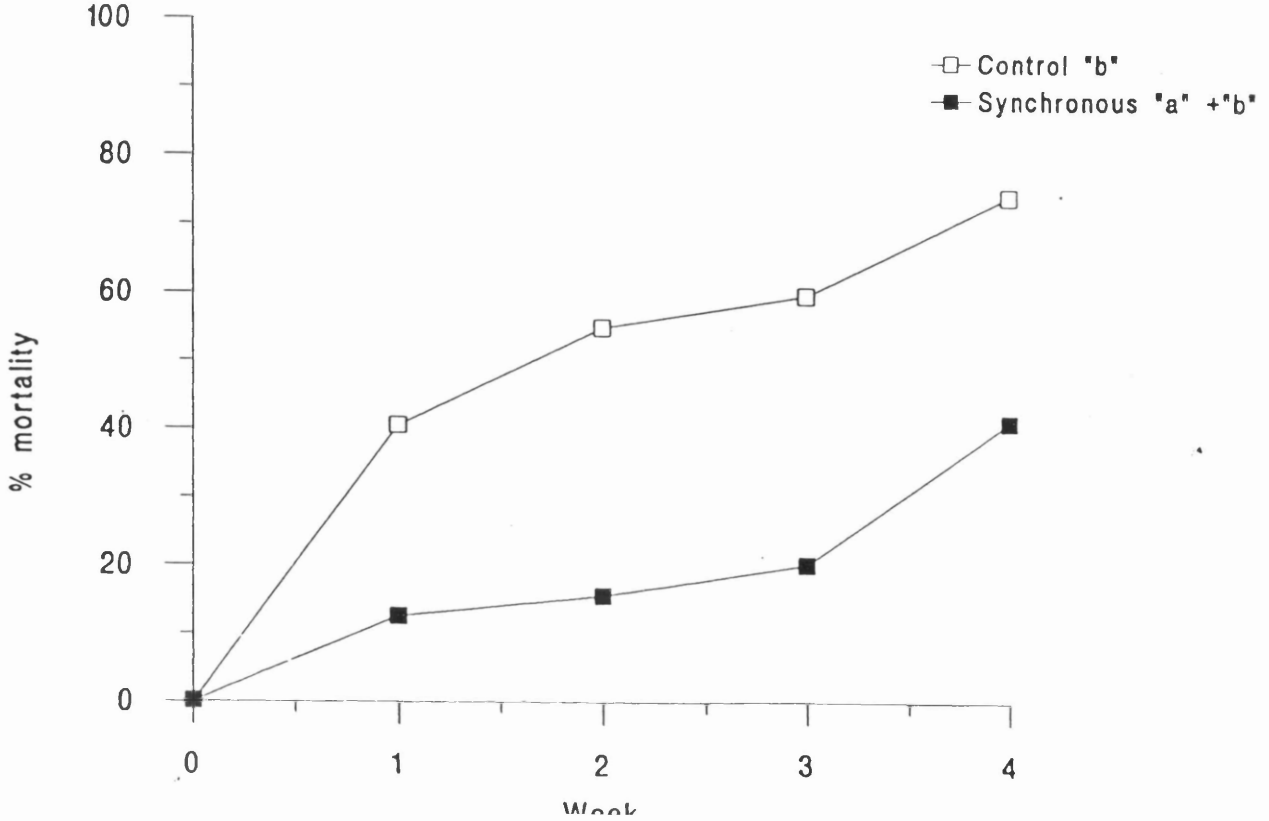

100
80
60
40
20
0
% mortality
0
1
2
3
4
Week
Control "b"
Synchronous "a" +"b"

Figure 8.1c Cumulative mortality to 4 weeks post-hatch of "c" chicks from control broods and from synchronous-hatching broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=1.17, N.S.).

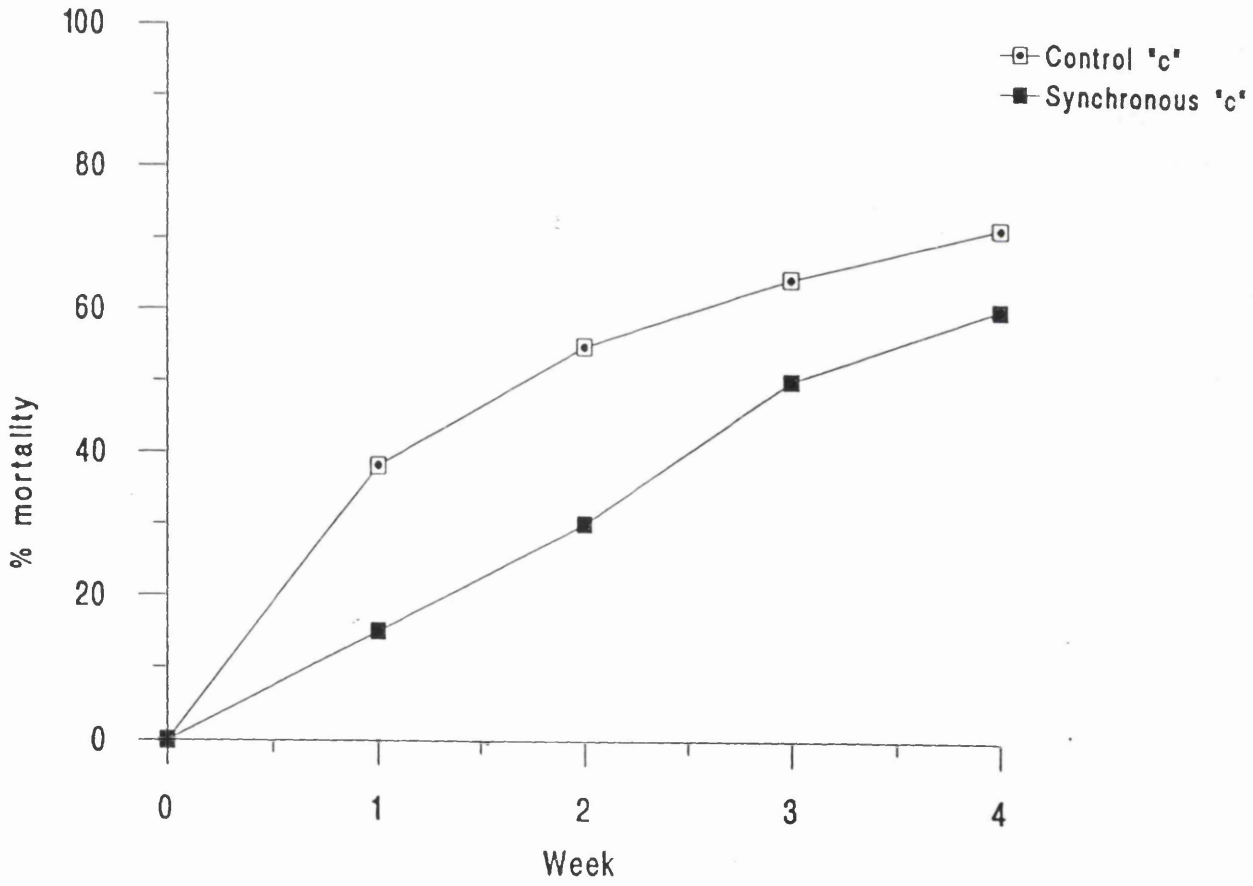

100
80
60
40
20
0
% mortality
0
1
2
3
4
Week
Control "c"
Synchronous "c"

Table 8.2 - Comparison of chick growth between chicks from experimental synchronous hatching broods, and unmanipulated asynchronous hatching broods. Walney 1990.

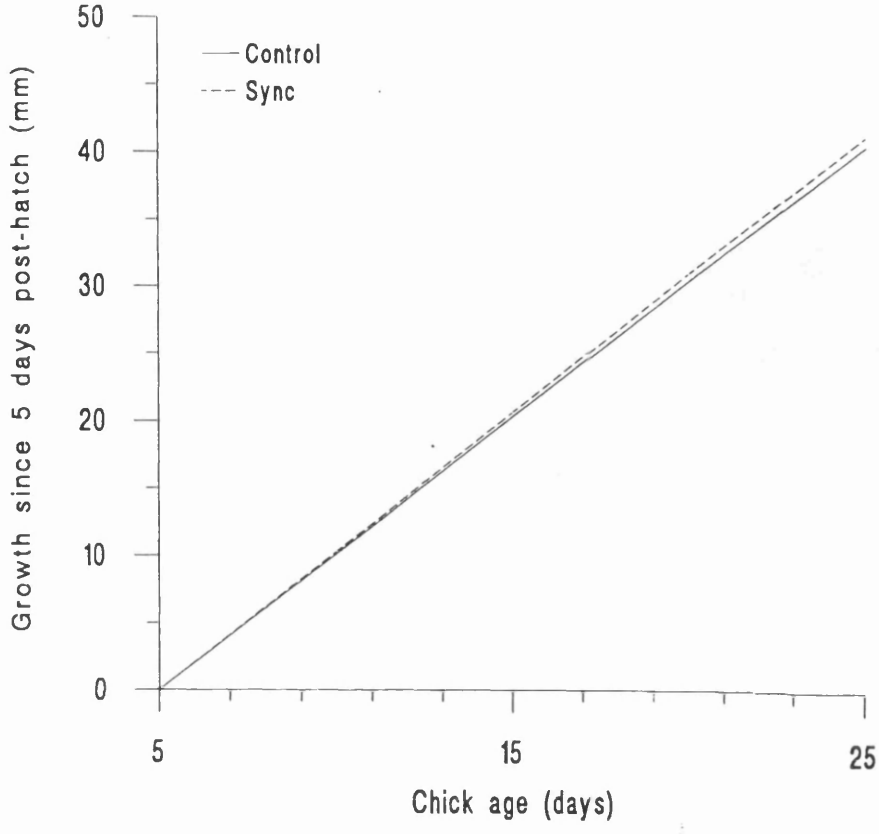
		Control			Synchronous			Differ-	Signif-
Measure	Chick	b=	r=	n=	b=	r=	n=	ence	icance
Head + Bill (mm/day)	A	2.030	0.990	11	2.067	0.991	22*	0.037	n.s.
	B	1.971	0.983	11				0.096	n.s.
	C	1.781	0.987	11	2.069	0.979	7	0.288	P<0.01
Weight (g/day)	A	3.077	0.980	11	3.050	0.983	22*	0.027	n.s.
	B	2.904	0.977	11				0.146	P<0.05
	C	2.480	0.968	11	2.806	0.958	7	0.326	P<0.01

Growth rates analysed by regression of measure against chick age between 0 and 28 days post-hatch. A and B chicks combined as they could not be accurately identified in synchronous-hatching broods.
Covariance results from SPSSX MANOVA procedure (Anon. 1988)
* - A and B chicks from synchronous broods combined for analysis.

Figure 8.2a Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "a" chicks from asynchronous hatching control broods and combined "a" and "b" chicks from synchronous-hatching broods, Walney 1990.

Figure 8.2b Comparison of rate of weight gain from 5 to 25 days post-hatch between "a" chicks from asynchronous hatching control broods and combined "a" and "b" chicks from synchronous-hatching broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.


Control
Sync
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

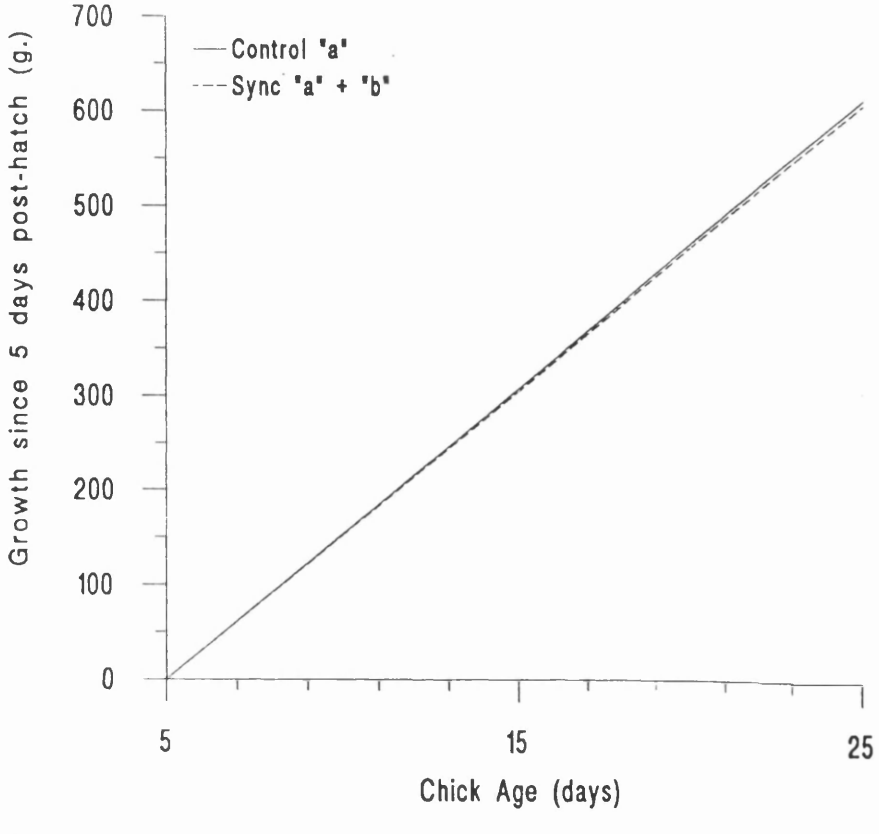
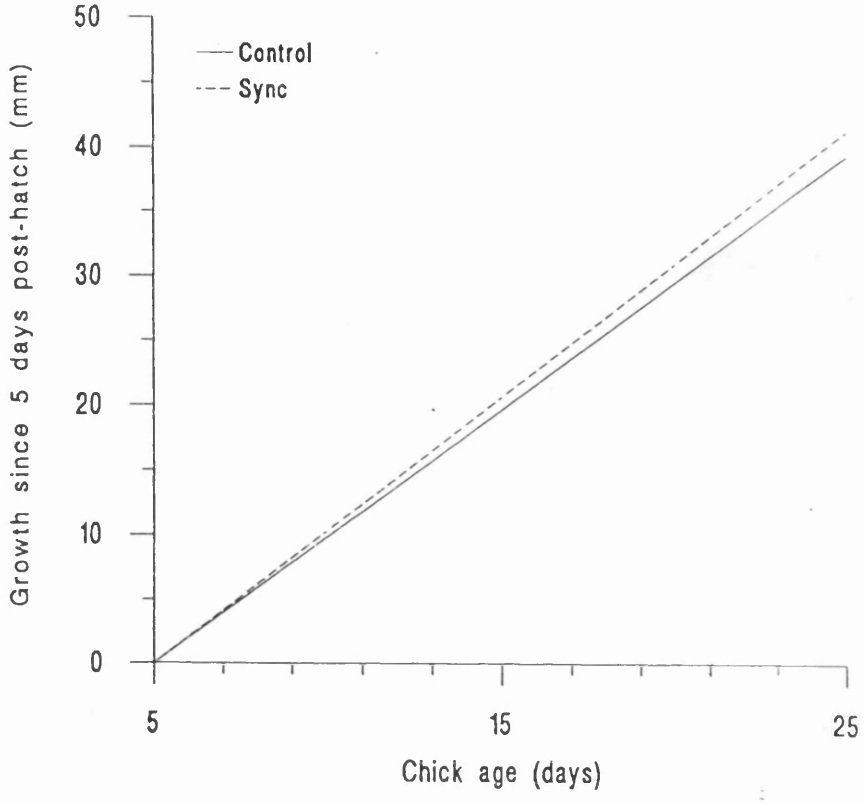

Control "a"
Sync "a" + "b"
Growth since 5 days post-hatch (g.)
700
600
500
400
300
200
100
0
5
15
25
Chick Age (days)

Figure 8.2c Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "b" chicks from asynchronous hatching control broods and combined "a" and "b" chicks from synchronous-hatching broods, Walney 1990.

Figure 8.2d Comparison of rate of weight gain from 5 to 25 days post-hatch between "b" chicks from asynchronous hatching control broods and combined "a" and "b" chicks from synchronous-hatching broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.


Control
Sync
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

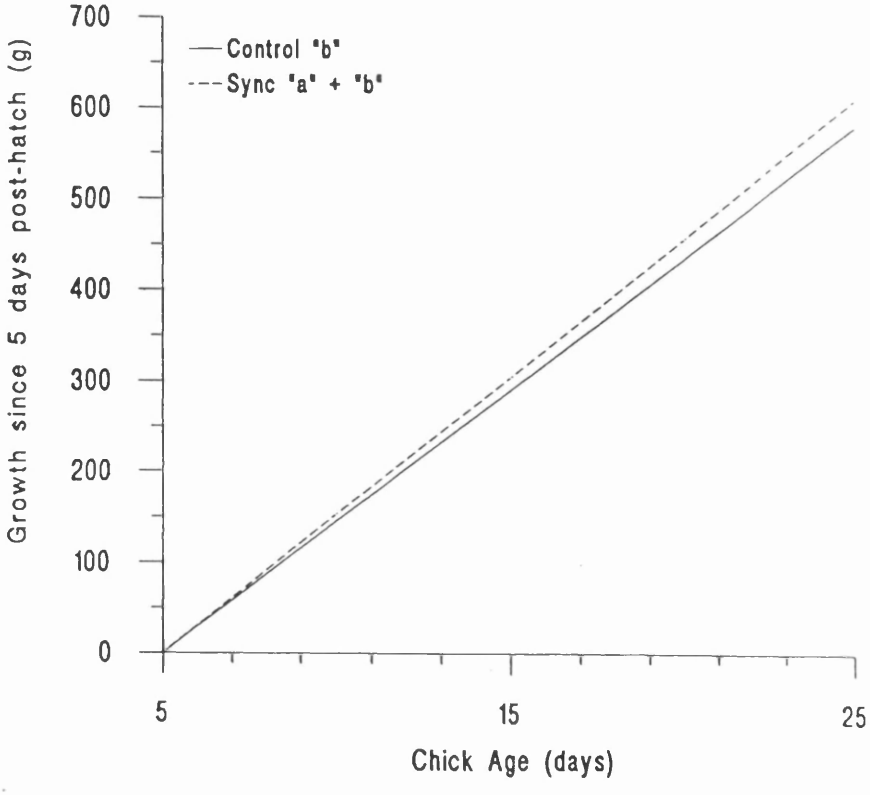
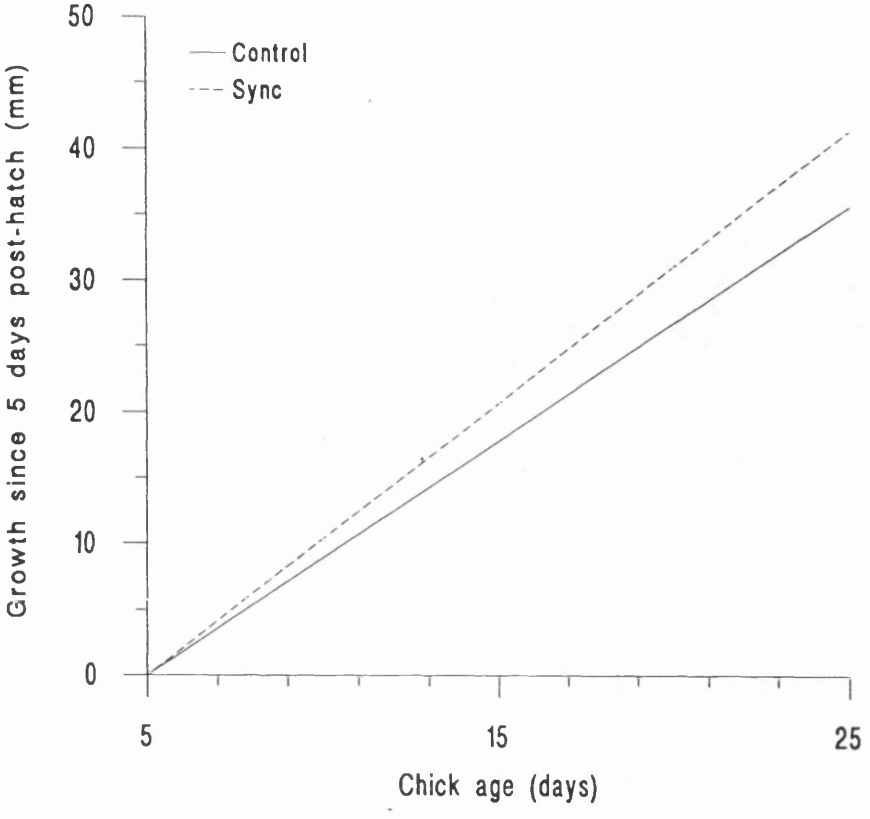

Control "b"
Sync "a" + "b"
Growth since 5 days post-hatch (g)
700
600
500
400
300
200
100
0
5
15
25
Chick Age (days)

Figure 8.2e Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "c" chicks from asynchronous hatching control broods and "c" chicks from synchronous-hatching broods, Walney 1990.

Figure 8.2f Comparison of rate of weight gain from 5 to 25 days post-hatch between "c" chicks from asynchronous hatching control broods and "c" chicks from synchronous hatching broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.


Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
Control
Sync
5
15
25
Chick age (days)

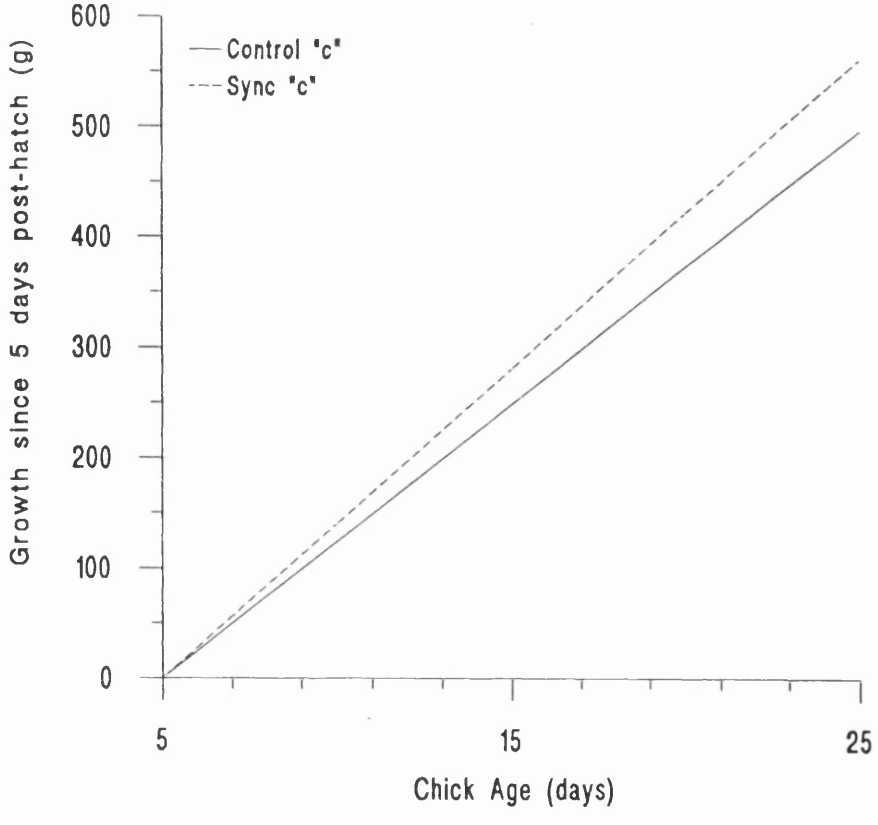
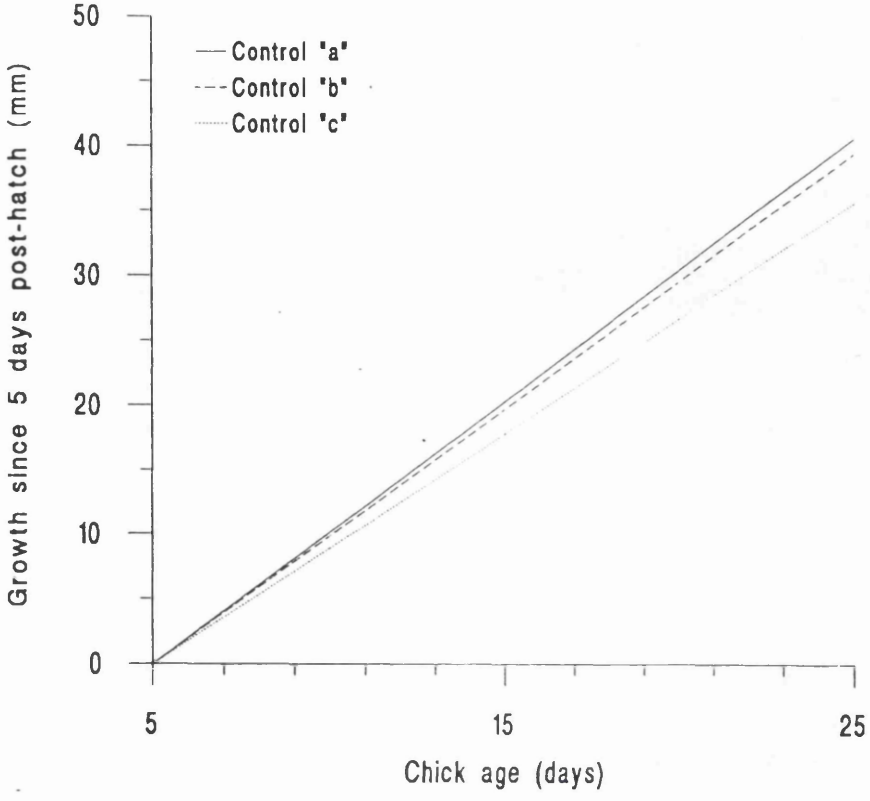

Growth since 5 days post-hatch (g)
600
500
400
300
200
100
0
Control "c"
Sync "c"
5
15
25
Chick Age (days)

Figure 8.2g Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between chicks from asynchronous hatching broods by hatch order, Walney 1990.

Figure 8.2h Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "c" chicks and combined "a" and "b" chicks from synchronous hatching broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.


Control "a"
Control "b"
Control "c"
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

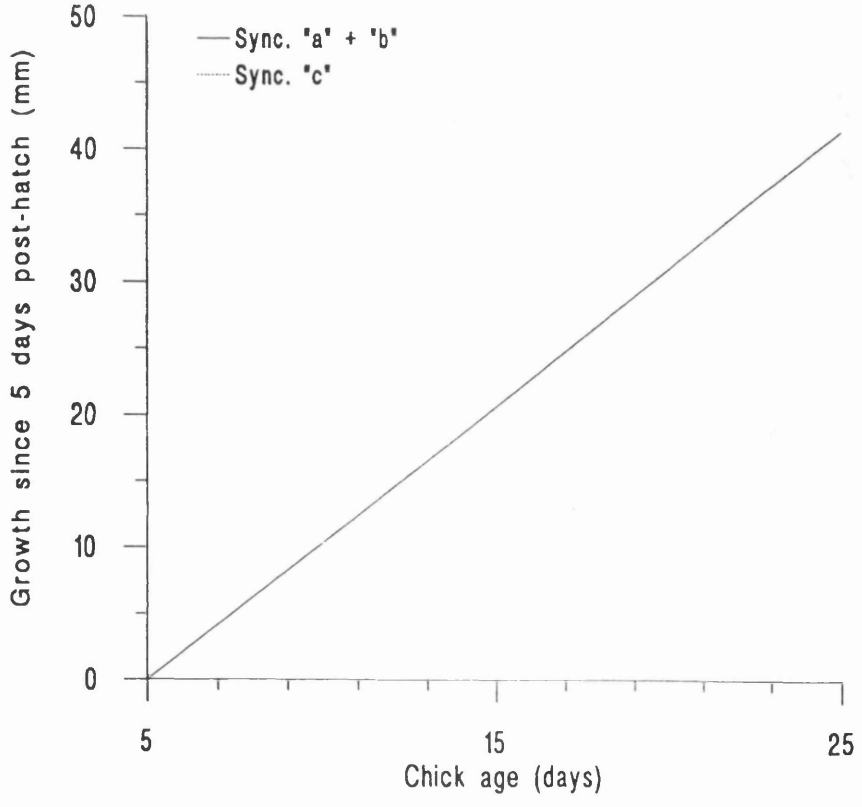
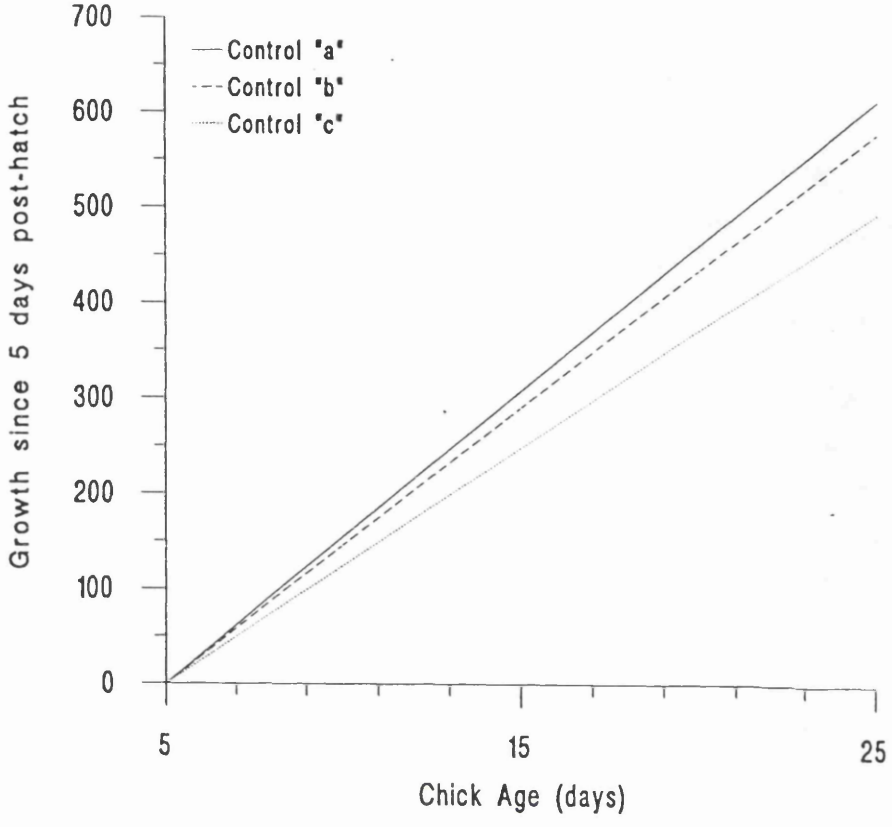
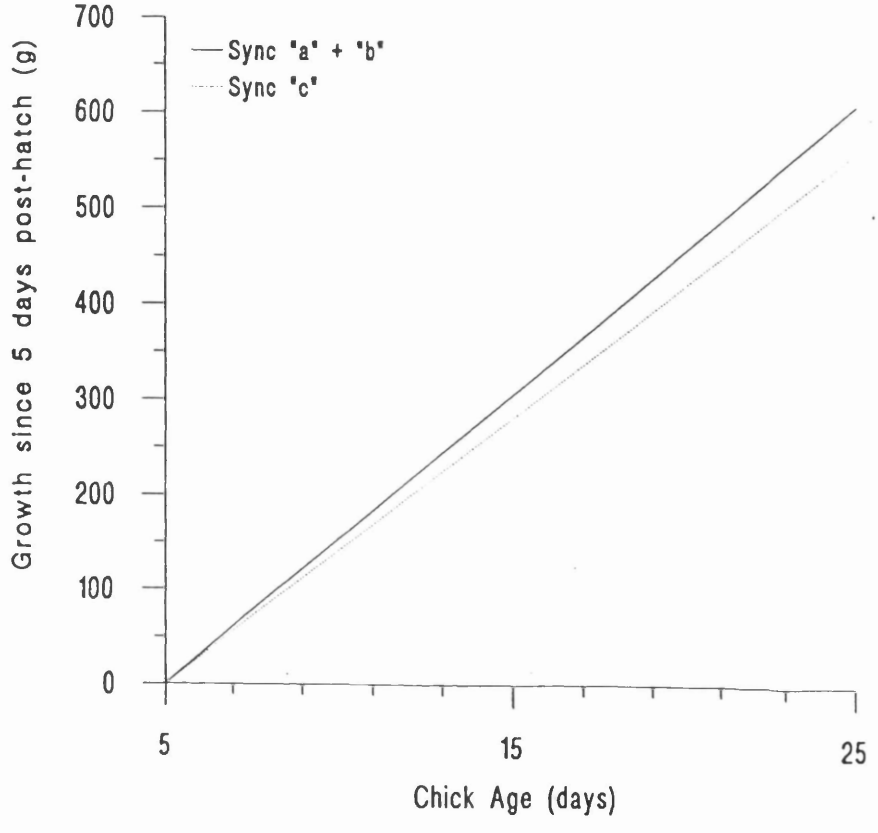

Sync. "a" + "b"
Sync. "c"
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

Figure 8.2i Comparison of rate of weight gain from 5 to 25 days post-hatch between chicks from asynchronous hatching broods, by hatch order, Walney 1990.

Figure 8.2j Comparison of rate of weight gain from 5 to 25 days post-hatch between "c" chicks and combined "a" and "b" chicks from synchronous-hatching broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in this analysis, plotting individual points produced less clear graphs.


Control "a"
Control "b"
Control "c"
Growth since 5 days post-hatch
700
600
500
400
300
200
100
0
5
15
25
Chick Age (days)


Sync "a" + "b"
Sync "c"
Growth since 5 days post-hatch (g)
700
600
500
400
300
200
100
0
5
15
25
Chick Age (days)

ble 8.3 Cumulative mortality of chicks from supplementary-fed broods and ntrol broods, to 4 weeks post-hatch, Walney 1990.

Colony	Chick	n=	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
Control	A	42	5 (11.9)	18 (42.9)	22 (52.4)	29 (69.0)
	B	42	17 (40.5)	23 (54.8)	25 (59.5)	31 (73.8)
	C	42	16 (38.1)	23 (54.8)	27 (64.3)	30 (71.4)
	Mean Brood Size	42	2.10	1.48	1.24	0.88
Supp. Fed	A	19	1 (5.3)	2 (10.5)	5 (26.3)	7 (26.3)
	B	19	1 (5.3)	3 (15.8)	7 (36.8)	10 (52.6)
	C	19	6 (31.6)	11 (57.9)	13 (68.4)	13 (68.4)
	Mean Brood Size	19	2.58	2.16	1.68	1.42

Comparison of survival to 4 weeks post-hatch between groups;
Control a with Supp. fed a - X^2 with Yates' correction=5.96, 1 d.f., $P<0.05$.
Control b with Supp. fed b - X^2 with Yates' correction=1.58, 1 d.f., N.S.
Control c with Supp. fed c - X^2 with Yates' correction<0.1, 1 d.f., N.S.

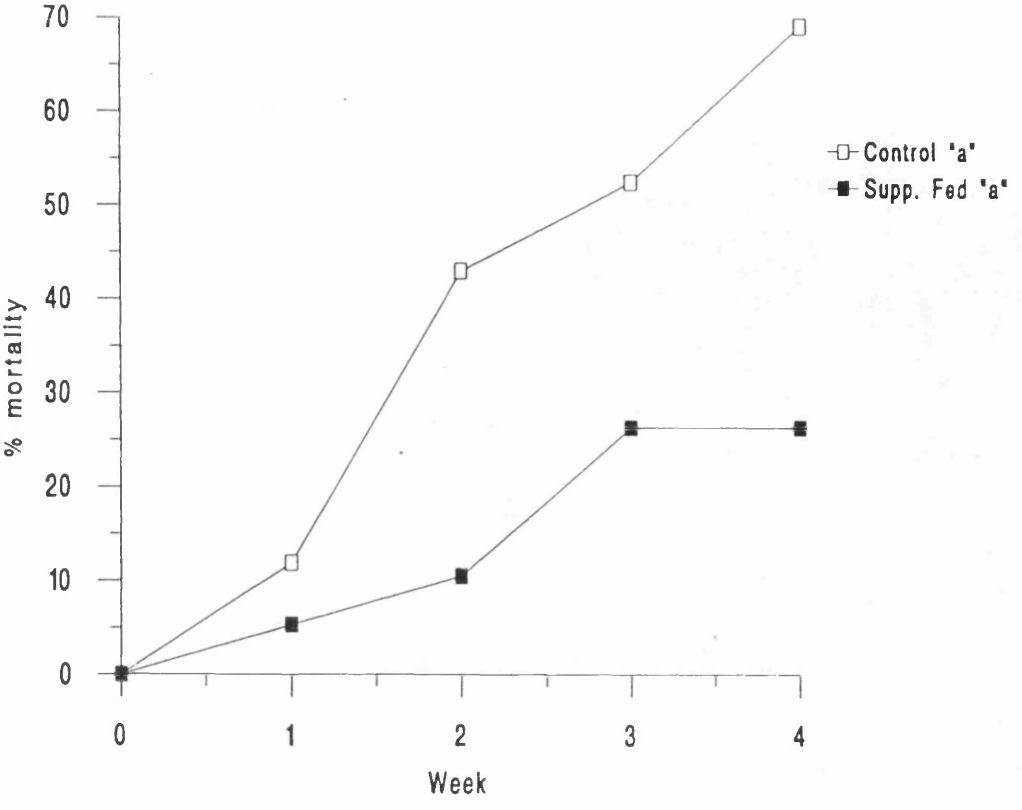
Comparison of survival per brood to 4 weeks post-hatch between groups;
Mann-Whitney U=287, $n_1=42$, $n_2=19$, $P<0.05$.

Figure 8.3a Cumulative mortality to 4 weeks post-hatch of "a" chicks from control broods and supplementart-fed broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=0.88, N.S.).

Figure 8.3b Cumulative mortality to 4 weeks post-hatch of "b" chicks from control broods and supplementary-fed broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=1.19, N.S.).


70
60
50
40
30
20
10
0
% mortality
0
1
2
3
4
Week
Control "a"
Supp. Fed "a"

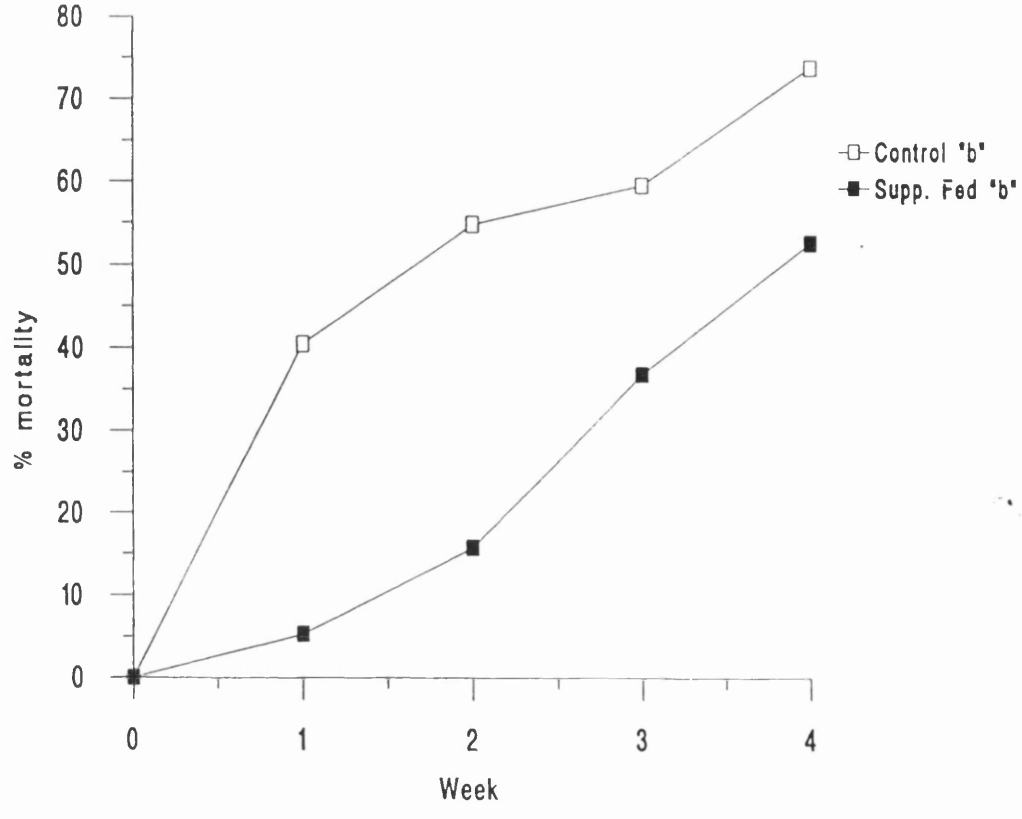
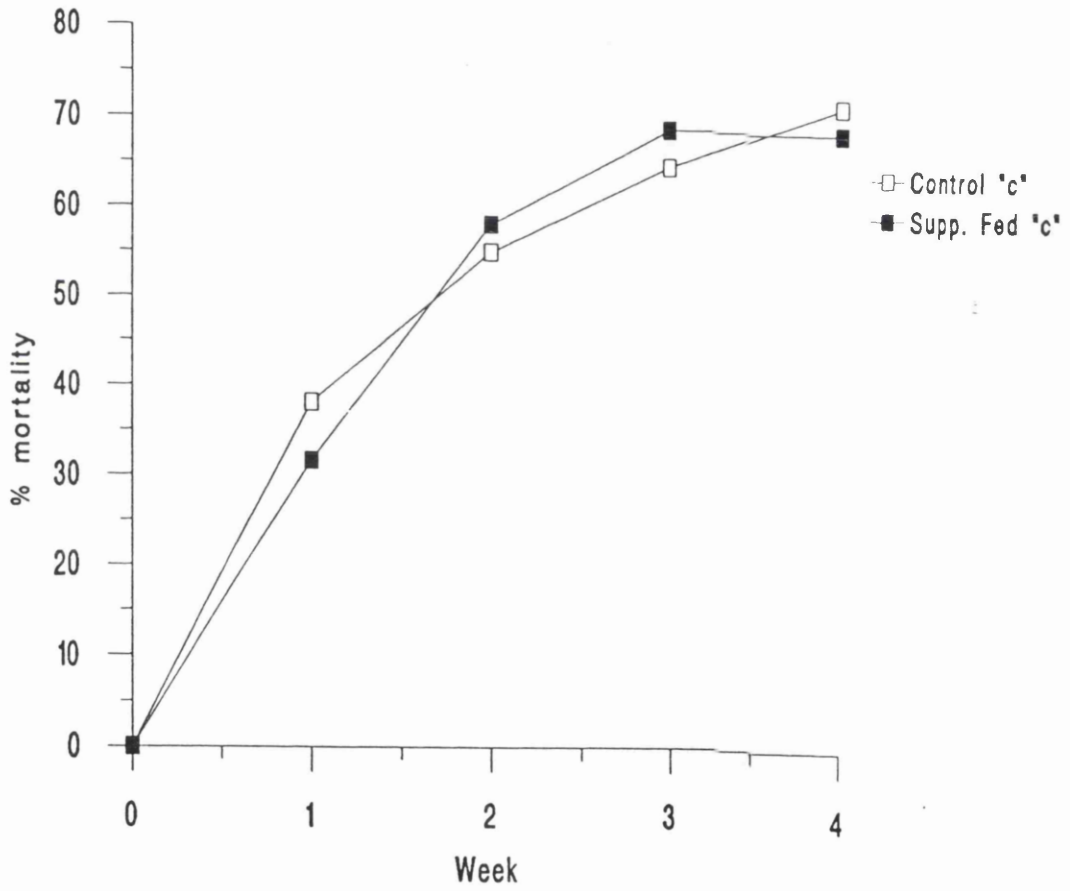

80
70
60
50
40
30
20
10
0
% mortality
0
1
2
3
4
Week
Control "b"
Supp. Fed "b"

Figure 8.1c Cumulative mortality to 4 weeks post-hatch of "c" chicks from control broods and from supplementary-fed broods.

Pattern of mortality not different (Kolmogorov-Smirnov Z=1.19, N.S.).


80
70
60
50
40
30
20
10
0
% mortality
0
1
2
3
4
Week
Control 'c'
Supp. Fed 'c'

combined *a* and *b* chicks (*a* - $F_{1,136}$=6.97, P<0.05).

Effect of delayed incubation on the hatching success of a eggs

Of the 66 *a* eggs replaced for 48hrs. with "dummy" eggs, 58 survived in the nests until they were due to hatch. Of these, only 44 hatched (75.9%). The combined hatching success of *b* and *c* eggs that survived until they were due to hatch was 99%, with only one egg failing to hatch from 102 eggs. These hatching successes were different (X^2 with Yates' correction = 20.9, 1 d.f., P<0.01).

8.4.3 - Effect of supplementary feeding during the first week post-hatch on chick survival and growth.

Chicks from broods that were supplementary fed showed higher survival at the end of week one than did the control group, with a higher survival rate for *b* chicks (X^2 with Yates' correction = 6.18, 1 d.f., P<0.05 Table 8.3), and larger brood size (Mann-Whitney n_1=42, n_2=20, U=269, P=0.01. Table 8.3). This difference continued until four weeks post-hatch; brood size being larger in week 2 (Mann-Whitney n_1=42 n_2=20 U=277, P<0.05), approaching significance in week 3 (Mann-Whitney n_1=42 n_2=20 U=304 P<0.1), and larger in week 4 (Mann-Whitney n_1=42, n_2=20, U=287, P<0.05). Survival of *a* chicks to four weeks post-hatch was higher in the supplementary fed group (Table 8.3), however there was no difference between groups in the survival of either the *b* or *c* chicks (Table 8.3). Timing of chick mortality did not differ between the groups for any chick in the hatch order (Kolmogorov-Smirnov test, *a* chicks - Z=0.88, N.S., *b* chicks - Z=1.19, N.S., *c* chicks - Z=0.47, N.S.).

Within treatments, hatching order had no effect on the proportion of chicks surviving to 4 weeks post-hatch (Control - X^2=0.233, 2 d.f., N.S. Supp. Fed - X^2=3.80, 2 d.f., N.S. Table 8.3).

The results of the growth rate analysis and comparisons between experimental groups are

Table 8.4 - Growth rates of chicks from supplementary fed broods and control broods Walney 1990.

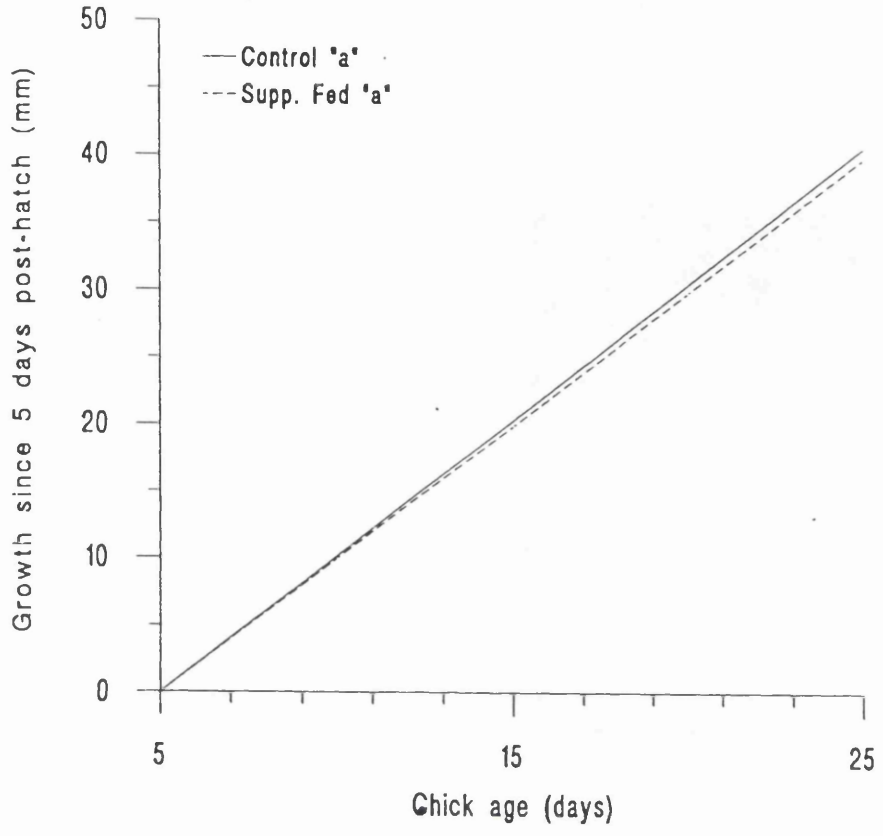
Measure	Chick	Control b=	Control r=	Control n=	Supplementary Fed b=	Supplementary Fed r=	Supplementary Fed n=	Difference	Significance
Head + Bill (mm/day)	A	2.030	0.990	11	1.990	0.984	10	0.040	n.s.
	B	1.971	0.983	11	1.930	0.984	9	0.041	n.s.
	C	1.781	0.987	11	1.957	0.979	7	0.176	P<0.01
Weight (g/day)	A	3.077	0.980	11	3.033	0.976	10	0.044	n.s.
	B	2.904	0.977	11	2.911	0.969	9	0.007	n.s.
	C	2.480	0.968	11	2.586	0.958	7	0.106	P<0.05

Growth rates measured by regression of measure against chick age between 5 and 25 days post-hatch.
Covariance results from SPSSX MANOVA procedure (Anon 1988).

Figure 8.2a Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "a" chicks from supplementary-fed broods and from control broods, Walney 1990.

Figure 8.2b Comparison of rate of weight gain from 5 to 25 days post-hatch between "a" chicks from supplementary-fed broods and from control broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in these analyses plotting individual points produced less clear graphs.


Control 'a'
Supp. Fed 'a'
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

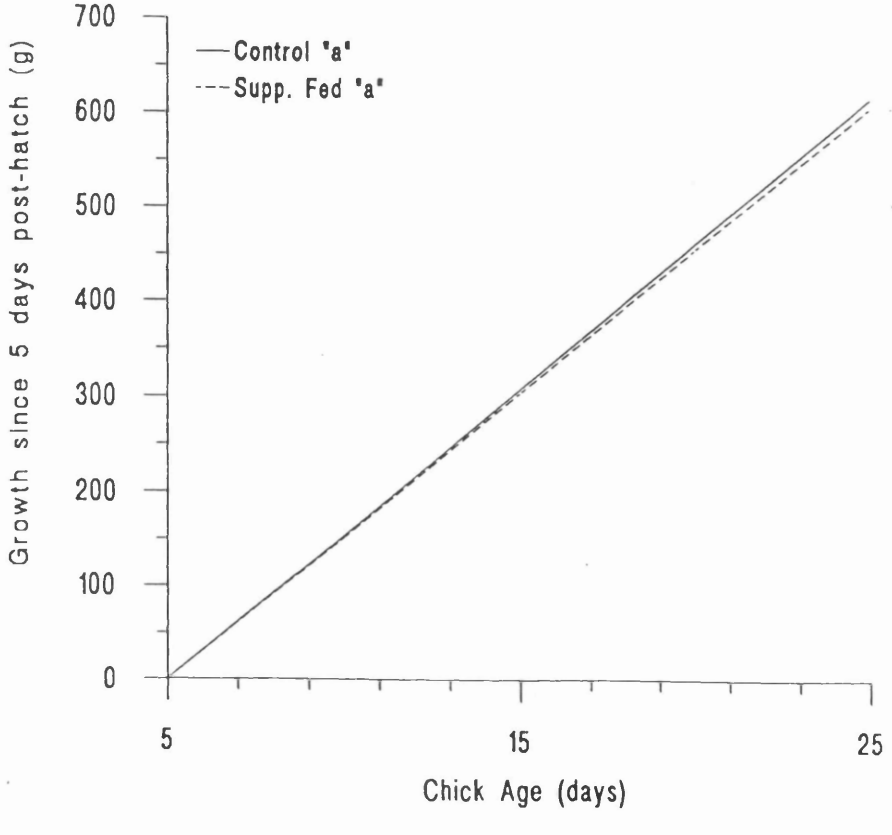
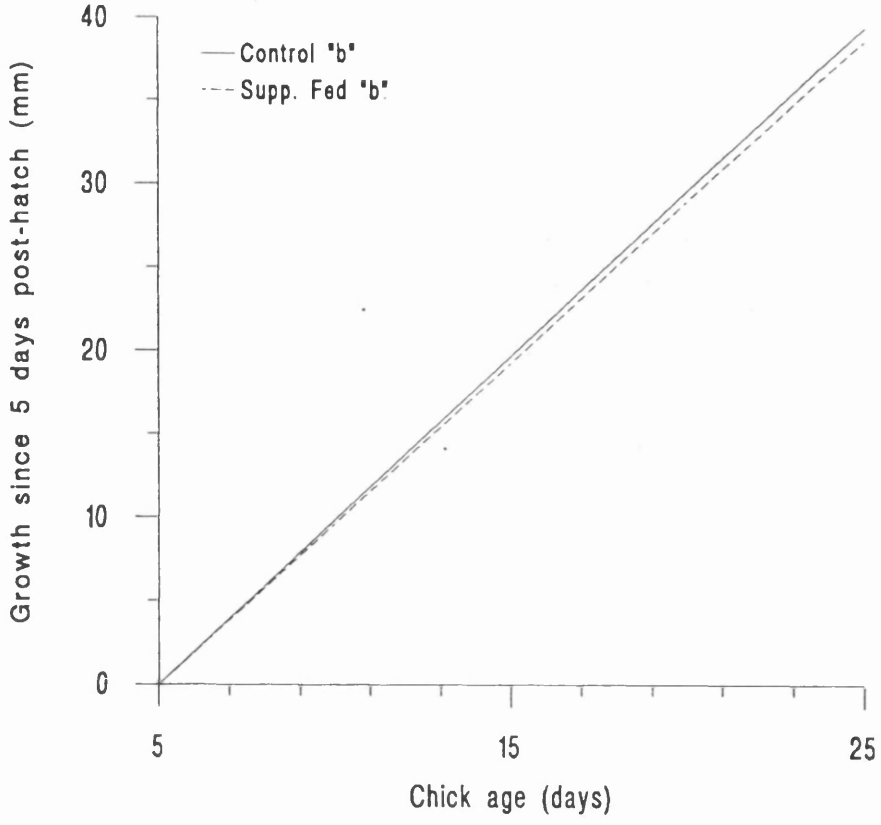

Control 'a'
Supp. Fed 'a'
Growth since 5 days post-hatch (g)
700
600
500
400
300
200
100
0
5
15
25
Chick Age (days)

Figure 8.2a Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "b" chicks from supplementary-fed broods and from control broods, Walney 1990.

Figure 8.2d Comparison of rate of weight gain from 5 to 25 days post-hatch between "b" chicks from supplementary-fed broods and from control broods, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in these analyses plotting individual points produced less clear graphs.


Growth since 5 days post-hatch (mm)
40
30
20
10
0
Control "b"
Supp. Fed "b"
5
15
25
Chick age (days)

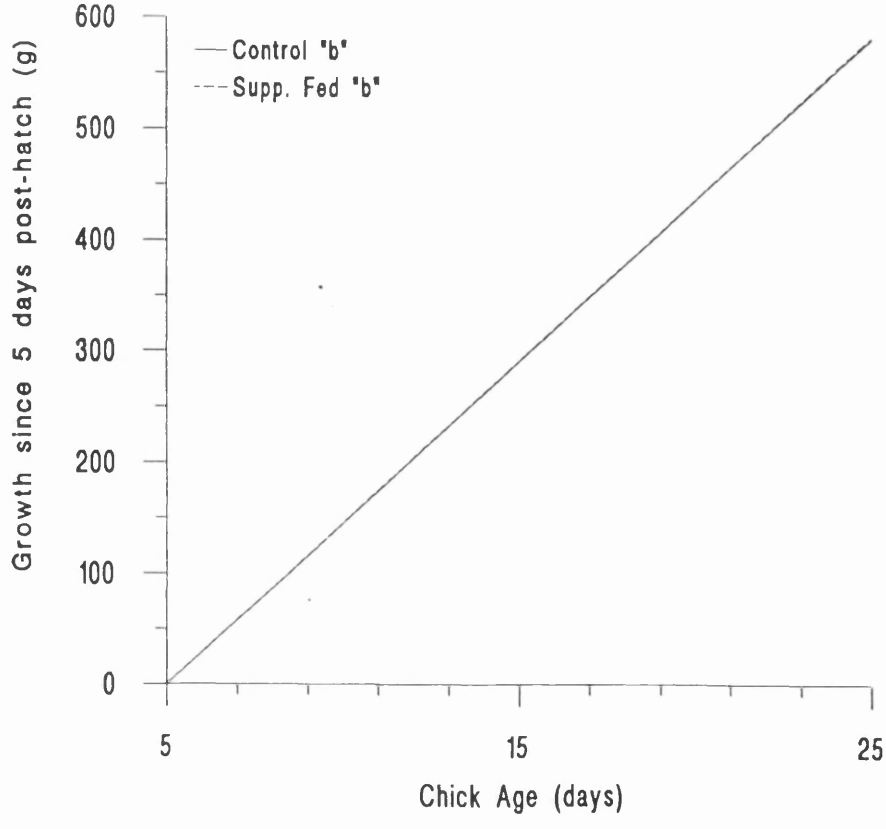
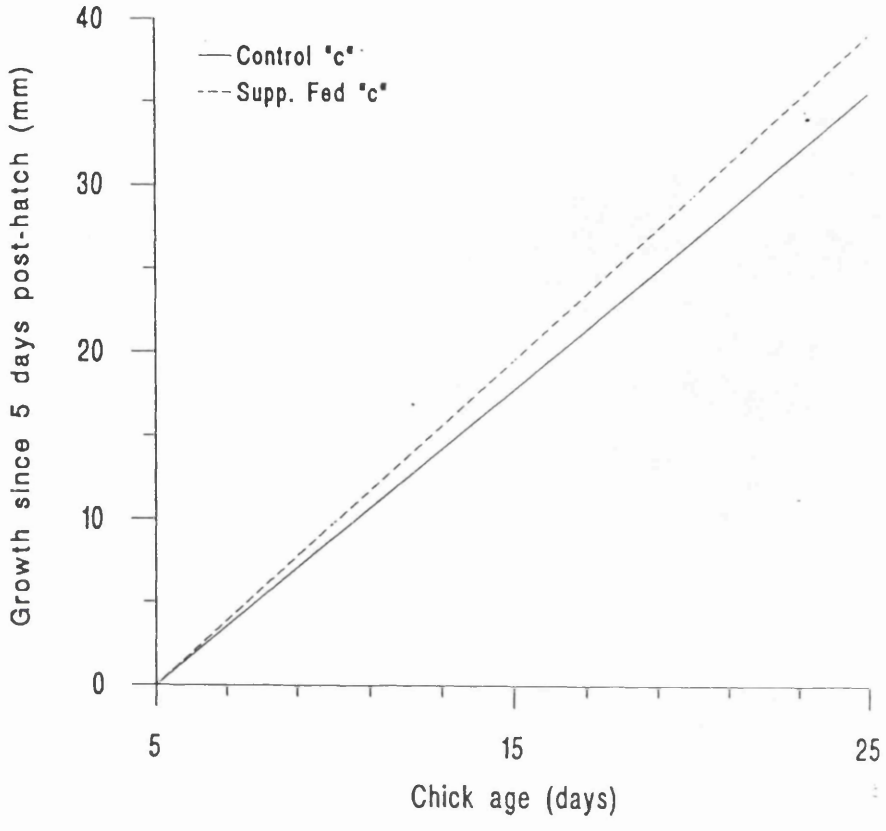

Growth since 5 days post-hatch (g)
600
500
400
300
200
100
0
Control "b"
Supp. Fed "b"
5
15
25
Chick Age (days)

Figure 8.2e Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between "c" chicks from supplementary-fed broods and from control broods, Walney 1990.

Figure 8.2f Comparison of rate of weight gain from 5 to 25 days post-hatch between "c" chicks from supplementary-fed broods and from control broods, Walney 1990. .pa

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in these analyses plotting individual points produced less clear graphs.


Growth since 5 days post-hatch (mm)
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30
20
10
0
Control "c"
Supp. Fed "c"
5
15
25
Chick age (days)

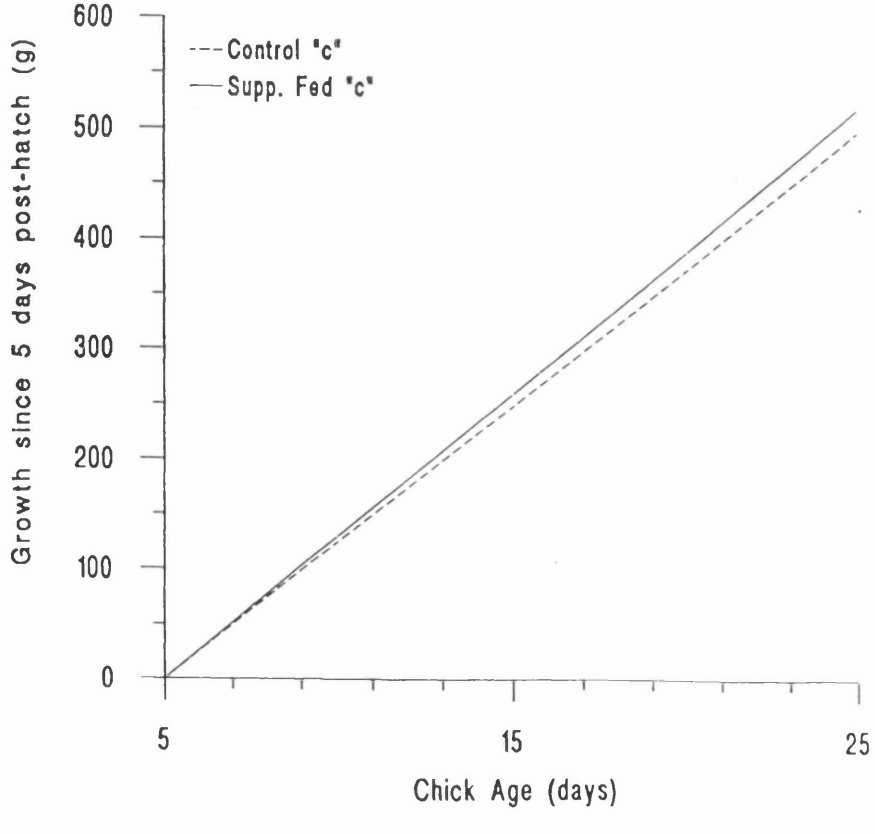
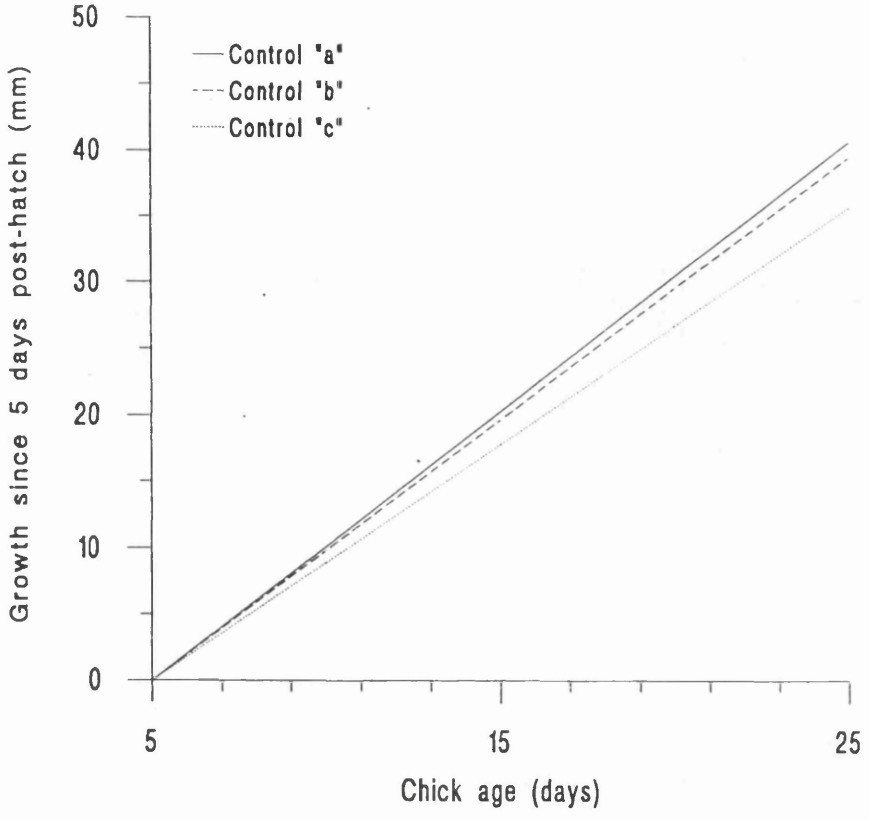

Growth since 5 days post-hatch (g)
600
500
400
300
200
100
0
Control "c"
Supp. Fed "c"
5
15
25
Chick Age (days)

Figure 8.2g Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between chicks from control broods by hatch order, Walney 1990.

Figure 8.2h Comparison of growth of Total Head and Bill length from 5 to 25 days post-hatch between chicks from supplementary-fed broods by hatch order, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in these analyses plotting individual points produced less clear graphs.


Control "a"
Control "b"
Control "c"
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)

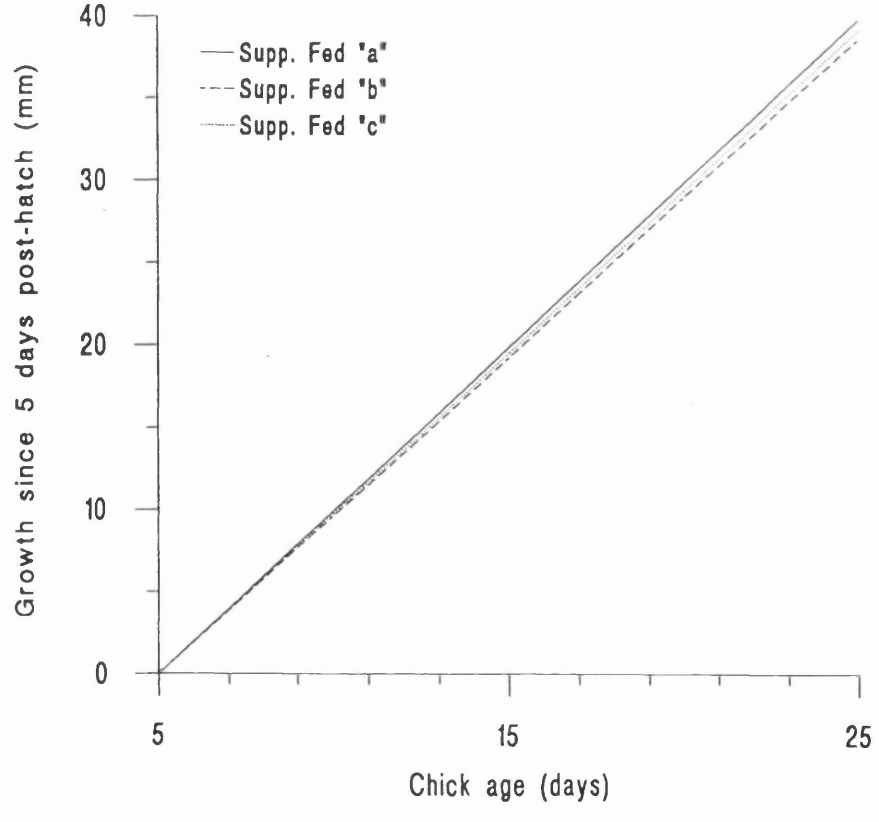
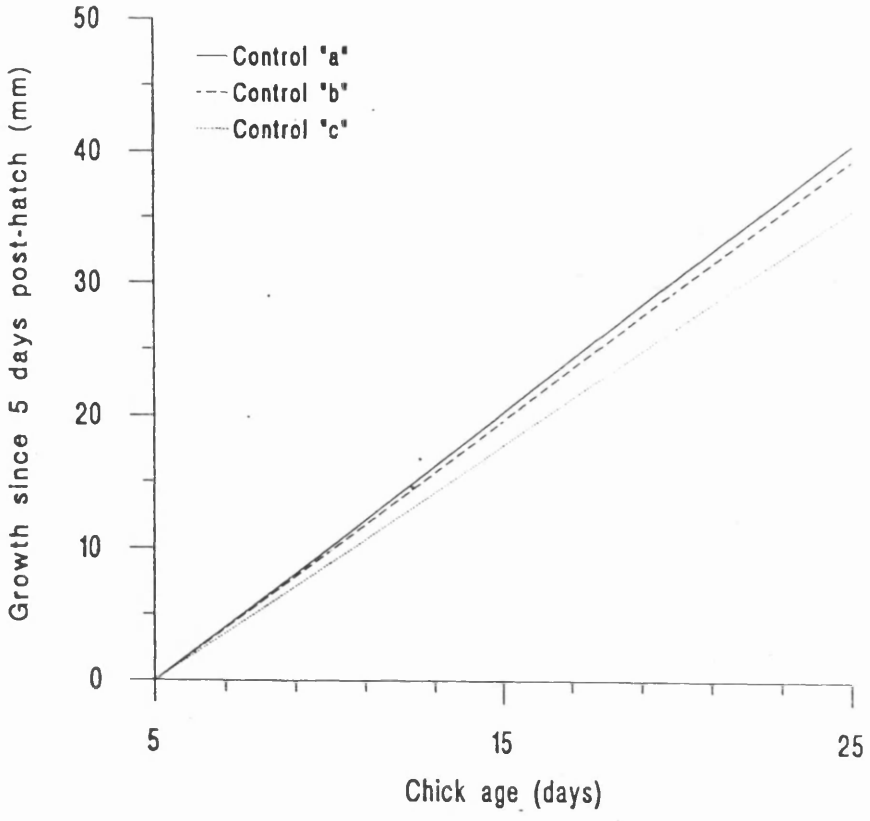
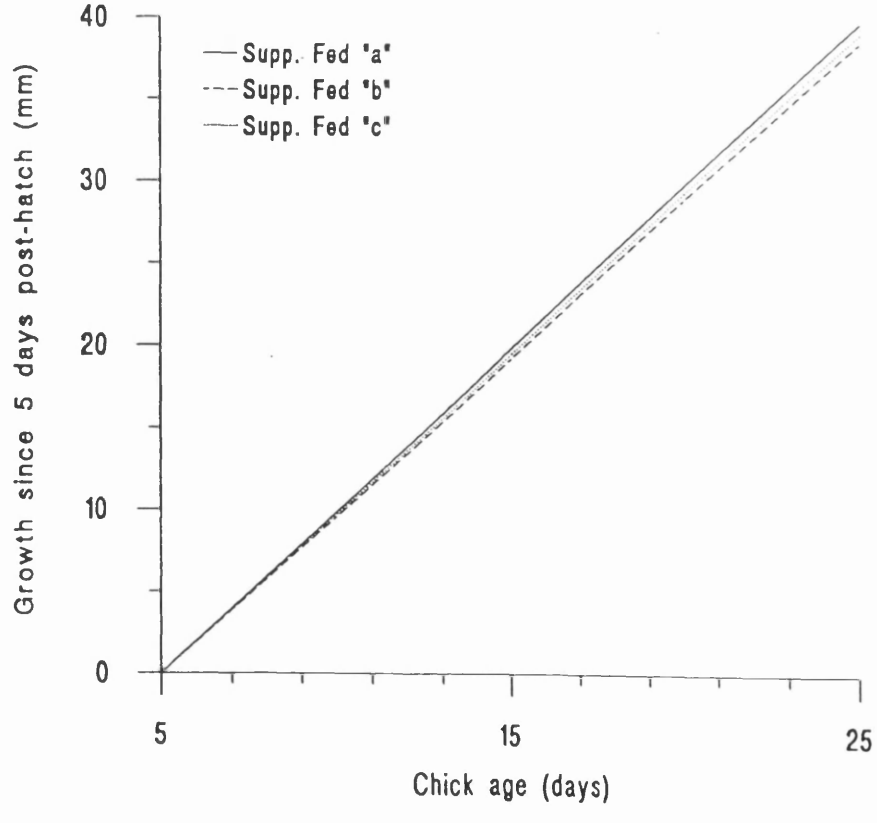

Supp. Fed "a"
Supp. Fed "b"
Supp. Fed "c"
Growth since 5 days post-hatch (mm)
40
30
20
10
0
5
15
25
Chick age (days)

Figure 8.2i Comparison of rate of weight gain from 5 to 25 days post-hatch between chicks from control broods by hatch order, Walney 1990.

Figure 8.2j Comparison of rate of weight gain from 5 to 25 days post-hatch between chicks from supplementary-fed broods by hatch order, Walney 1990.

N.B. For the sake of clarity, only mean growth rates for each group are shown. With the large sample sizes involved in these analyses plotting individual points produced less clear graphs.


Control "a"
Control "b"
Control "c"
Growth since 5 days post-hatch (mm)
50
40
30
20
10
0
5
15
25
Chick age (days)


Supp. Fed "a"
Supp. Fed "b"
Supp. Fed "c"
Growth since 5 days post-hatch (mm)
40
30
20
10
0
5
15
25
Chick age (days)

presented in Table 8.4 and Figure 8.4. Within treatments, no differences were found in growth rates between *a* and *b* chicks (Slope comparisons by Covariance analysis. Control - T.H.B., $F_{1,158}=0.72$, N.S. Weight - $F_{1,158}=2.29$, N.S. Supplementary fed - T.H.B., $F_{1,96}=0.29$ N.S. Weight, $F_{1,96}=1.51$ N.S.).

C chicks grew more slowly than did the *a* and *b* chicks in each treatment (Slope comparisons by Covariance analysis. Control *a* - T.H.B., $F_{1,172}=8.97$, $P<0.01$. Weight, $F_{1,172}=24.14$, $P<0.01$. Control *b* - T.H.B., $F_{1,172}=7.10$, $P<0.01$. Weight, $F_{1,172}=16.91$, $P<0.01$. Supplementary fed - *a* Weight, $F_{1,105}=15.90$, $P<0.01$. *b* Weight, $F_{1,99}=7.10$, $P<0.05$), except for growth of T.H.B. in supplementary fed *c* chicks where no difference was found (*a* $F_{1,105}=0.29$, N.S. *b* $F_{1,99}=0.02$, N.S.).

Between treatments, no differences were found between either *a* chicks (Slope comparisons by Covariance analysis. T.H.B., $F_{1,131}=0.72$, 1 d.f., $P>0.05$. Weight, $F_{1,131}=0.40$, 1 d.f., $P>0.05$.) or *b* chicks (T.H.B., $F_{1,135}=0.77$, 1 d.f., $P>0.05$. Weight, $F_{1,135}=0.04$, 1 d.f., $P>0.05$). *C* chicks from supplementary broods grew quicker than control *c* chicks (T.H.B., $F_{1,136}=7.73$, 1 d.f., $P<0.01$. Weight, $F_{1,136}=4.75$, 1 d.f., $P<0.05$).

8.4.4 - Adult attendance at supplementary fed nests and control nests

Matching the observations by time period resulted in no differences in distribution of watches in terms of time for any age group under observation (Week 1 $X^2= 9.845$, 7 d.f., N.S. Week 2 $X^2= 7.562$, 7 d.f., N.S. Week 3 $X^2=3.144$, 7 d.f., N.S. Week 4 $X^2=9.389$, 7 d.f., N.S.). During the first week post-hatch, the proportion of observations where no adults were present was higher in the control group than in the supplementary fed group (Figure 8.4).

The proportion of observations (scan samples of nests at 10 minute intervals) where two adults were present during the first week post-hatch was higher for the supplementary fed

Table 8.5 Nest attendance* split by chick age, for Control nests and nests where supplementary food was provided during the first week post-hatch.

Exp. Group	Nº of Adults	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
Control	0	248 (14.7)	8 (1.5)	0 (-)	2 (2.8)
	1	1242 (73.7)	444 (82.8)	128 (72.7)	54 (75.0)
	2	196 (11.6)	84 (15.7)	48 (27.3)	16 (22.2)
	n=	1686	536	176	72
Supp. Fed	0	152 (5.2)	10 (1.6)	2 (1.1)	0 (-)
	1	2203 (75.3)	556 (86.6)	154 (87.5)	36 (100)
	2	570 (19.5)	76 (11.8)	20 (11.4)	0 (-)
	n=	2925	642	176	36

* Nest attendance measured by scan samples of nests taken every 10 minutes. Figures in table represent number of scan sample records.

group than the control group (X^2 with Yates' correction = 122.19, 1 d.f., P<0.0001. (Figure 8.5). During the second week no difference was found in attendance of no adults (X^2 with Yates' correction <0.01, 1 d.f., P>0.1), however attendance by two adults approached significance (X^2 with Yates' correction = 3.33, 1 d.f., 0.1>P<0.05). During weeks 3 and 4, no difference was found between the groups in the proportion of observations where no adults were in attendance (Week 3 - X^2 with Yates' correction <0.01, 1 d.f., P>0.1. Week 4 - X^2 with Yates' correction <0.01, 1 d.f., P>0.1), however the proportion of observations where 2 adults were present was higher for the control group than for the supplementary fed group (Week 3 - X^2 with Yates' correction = 12.32, 1 d.f., P<0.01. Week 4 - X^2 with Yates' correction = 7.63, 1 d.f., P<0.01).

8.4.5 - Effect of brood age on adult attendance

In all time periods significant differences were found between different brood ages in both attendance of no adults on territory and of two adults on territory. The former decreased with brood age (Figure 8.6, Table 8.6), while the latter increased in all but one time period (Figure 8.7, Table 8.6).

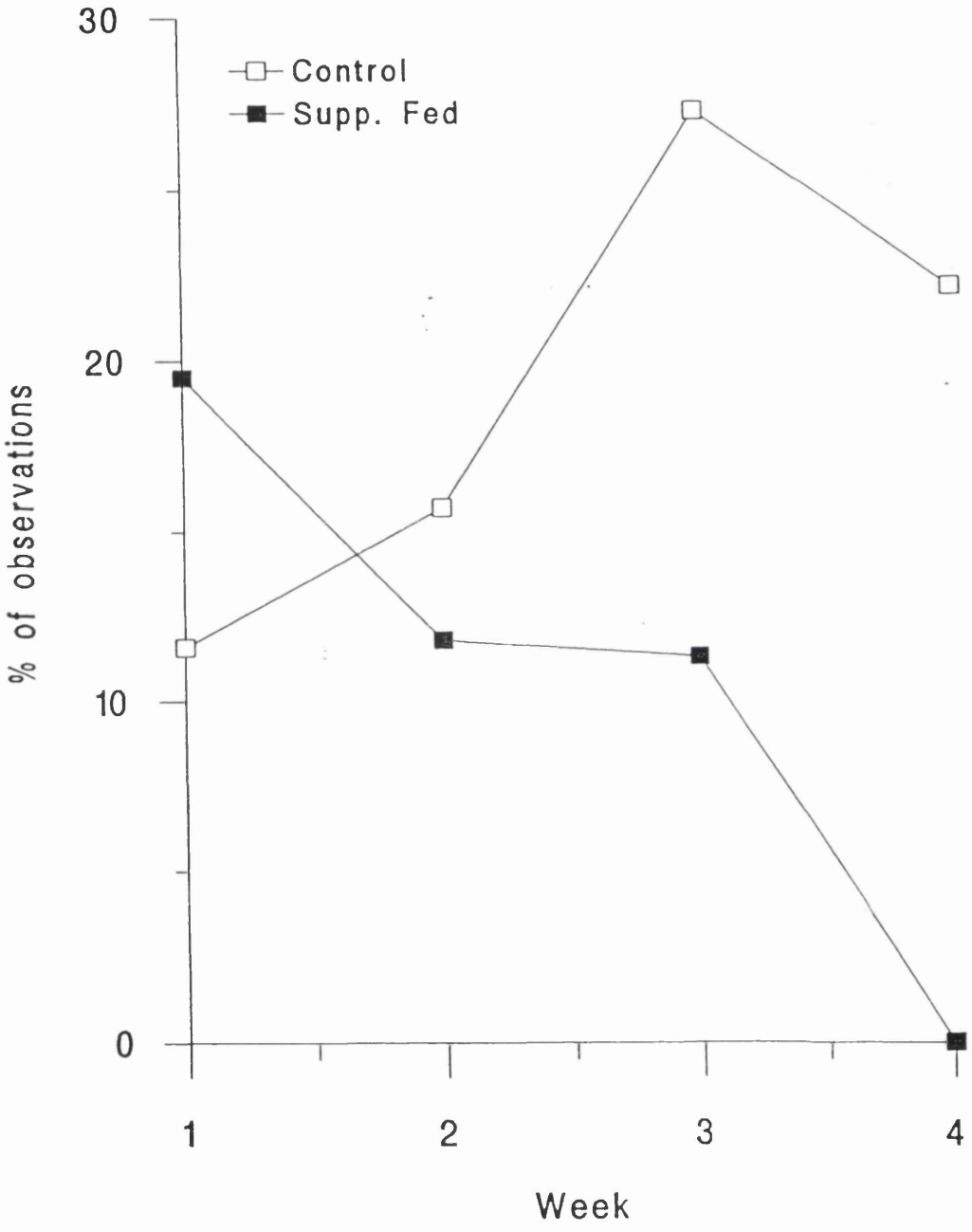
DISCUSSION

Effects of hatching synchrony

Hatching asynchrony in Herring gulls does not appear to be in itself adaptive as in this study, synchronous hatching broods showed increased fledging success per brood as a result of increased survival of *a* and *b* chicks. *B* and *c* chicks from synchronous broods gained weight at a faster rate than those from control broods, and synchronous brood *c* chicks had a higher growth rate for total head and bill than did control brood *c* chicks. No control chicks showed either increased growth rates or increased survival compared with the same chicks in the hatch order from synchronous hatching broods. Synchronous hatching appears to be advantageous for all chicks within a brood.

This finding is the opposite to that made by Hahn (1981) working with Laughing gulls

Figure 8.5b - Attendance by both adults simultaneosly at the nests of supplementary-fed broods and control broods, as measured by the percentage of scan samples taken evry 10 minutes, from 1 to 4 weeks post-hatch.



Comparison of proportion of observations where 2 adults were in attendance, between control and supplementary fed broods;
Week 1 - X^2 with Yates' correction = 34.4, 1 d.f., $P<0.001$
Week 2 - X^2 with Yates' correction = 3.3, 1 d.f., N.S.
Week 3 - X^2 with Yates' correction = 12.3, 1 d.f., $P<0.01$
Week 4 - X^2 with Yates' correction = 7.63, 1 d.f., $P<0.01$

Table 8.6a The numbers of nests with different numbers of adults observed on territory in 10 minute scan samples, with brood age (weeks post-hatch). Period 1 (05.00 - 09.59 hrs).

Brood Age (after hatching of first chick)

Nº of Adults	Week 1 (%)	Week 2 (%)	Week 3 (%)
0	11 (36.7)	40 (10.9)	0 (-)
1	19 (63.3)	228 (61.9)	66 (91.7)
2	0 (-)	100 (27.2)	6 (8.3)
n=	30	368	72

Table 8.6b The numbers of nests with different numbers of adults observed on territory in 10 minute scan samples, with brood age (weeks post-hatch). Period 2 (10.00 - 13.59 hrs).

Brood Age (after hatching of first chick)

Nº of Adults	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
0	8 (33.3)	7 (2.5)	6 (2.1)	14 (5.0)
1	16 (66.7)	251 (90.2)	254 (91.4)	216 (78.3)
2	0 (-)	20 (7.2)	18 (6.5)	46 (16.7)
n=	24	278	278	276

Table 8.6c The numbers of nests with different numbers of adults observed on territory in 10 minute scan samples, with brood age (weeks post-hatch). Period 3 (14.00 - 17.59 hrs).

Brood Age (after hatching of first chick)

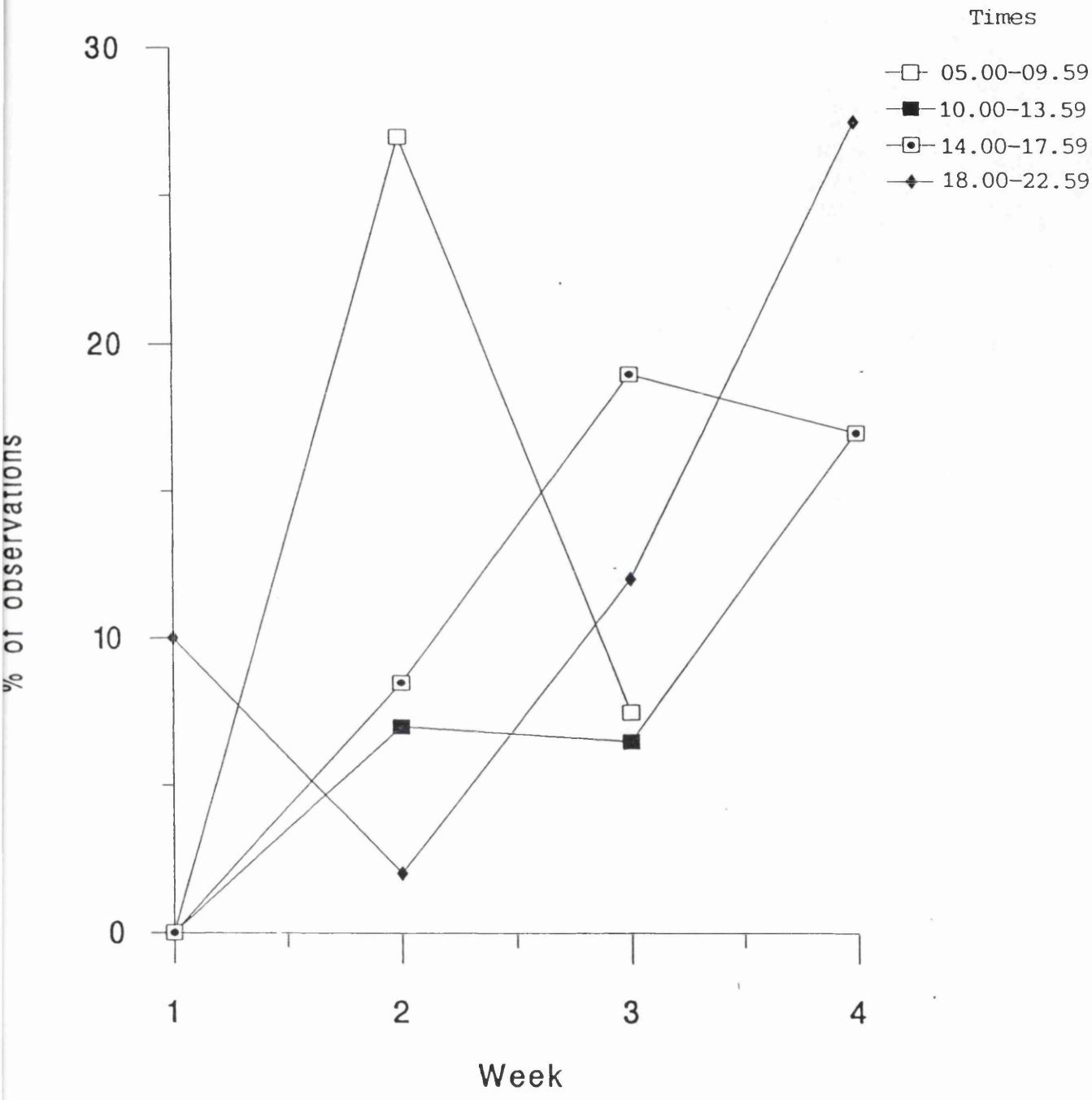
Nº of Adults	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
0	18 (75.0)	40 (6.0)	6 (1.7)	8 (5.6)
1	6 (25.0)	566 (85.5)	274 (78.7)	116 (80.5)
2	0 (-)	56 (8.5)	68 (19.5)	20 (13.9)
n=	24	662	348	144

Table 8.6a The numbers of nests with different numbers of adults observed on territory in 10 minute scan samples, with brood age (weeks post-hatch). Period 4 (18.00 - 22.59 hrs).

Brood Age (after hatching of first chick)

Nº of Adults	Week 1 (%)	Week 2 (%)	Week 3 (%)	Week 4 (%)
0	10 (16.4)	11 (6.4)	2 (0.9)	0 (-)
1	45 (73.8)	158 (91.9)	187 (86.6)	156 (72.2)
2	6 (9.8)	3 (1.7)	27 (12.5)	60 (27.8)
n=	61	172	216	216

Figure 8.7 Percentage of nest observations where 2 adults were in attendance, split by time of day from 1-4 weeks post-hatch



Comparison of attendance between different brood ages, for each period;

Period 1 - X^2=21.57, 2 d.f., P<0.001
Period 2 - X^2=22.93, 3 d.f., P<0.001
Period 3 - X^2=29.82, 3 d.f., P<0.001
Period 4 - X^2=53.61, 3 d.f., P<0.001

(*Larus atricapilla*). In that study, Hahn claims that synchronous-hatching broods fledged less young per brood than did control asynchronous broods. The data presented in that paper are however not convincing. The result that synchronous broods fledged less young per brood than asynchronous broods is based on a one-tailed X^2 test of the proportions of chicks that survived to fledging in each group. This test is inappropriate, as it assumes that all chicks within broods are independent. If the data presented in Hahn are re-analysed testing for a difference in the number of chicks fledged per brood, then the result is no longer significant (Mann-Whitney U=218, n_1=48, n_2=13, N.S.). There are also serious methodological flaws in Hahns experiment which could introduce serious biases into the results (see Chapter 7 Introduction).

Of the current hypotheses pertaining to hatching asynchrony in birds, none predict that synchronous hatching broods should fledge more young than asynchronous hatching broods. This is because they all assume that hatching asynchrony is a strategy employed by parents to maximise reproductive output. Asynchronous hatching clearly did not maximise reproductive output within a season in this study.

It is now widely assumed that evolution acts on animals to maximise lifetime reproductive success (L.R.S.) rather than success in any individual breeding bout (see Newton 1990 for a review of avian examples). It is possible that increasing breeding success within a single breeding bout could reduce L.R.S. by increasing an animal's chance of mortality, or by affecting an animals subsequent breeding efforts. It is therefore possible that asynchronous hatching is adaptive and that the increased fledging success from synchronous hatching broods has an overall negative effect on L.R.S.

The finding that breeding gulls are capable of rearing far larger broods than the usual three (e.g. Vermeer 1963, Ward 1973), suggests that the increased "strain" placed on breeding adults through rearing a synchronous hatching brood would be unlikely to have any major effect on the adults. Whilst these studies did not study subsequent adult mortality, the fact that they showed that some adults were capable of rearing broods of up

to 7 chicks to fledging, suggests that the difference between rearing 0.88 chicks and 1.60 chicks would be unlikely to have sufficient survival consequences on the adults to negate the large increase in fledging success.

The E.B.H. predicts that asynchronous hatching should result in adults having to switch chick diet at a time when either the oldest or youngest chicks should be placed at a disadvantage. Adults could change diet when the *a* and *b* chicks are old enough to switch, in which case the *c* chick would than receive an inappropriate diet (on average for 2.8 days if the switch was controlled by the age of the *a* chick, 2.8 days is the mean hatching span (MacRoberts and MacRoberts 1972)). Alternatively adults could switch when the *c* chick is old enough, in which case the *a* and *b* chicks would be placed at a disadvantage as a result of being fed "Expensive Babyfood" when they could have switched to prey that would increase the rate of energy/nutrient delivery. The results of this experiment suggest that adults must trade-off the survival of all chicks with regards to the timing of the prey switch, as all chicks in the hatching order showed increased survival or growth rates. If adults favoured the *a* and *b* when switching i.e. switched when they were old enough, then one would not expect the *a* and *b* to show any differences in survival between the synchronous hatching broods and the control broods (as in both cases the switch would occur at the optimal time for *a* and *b* chicks). If adults wait until the *c* chick is old enough before switching, then there could still be a difference in *c* chick growth rates between the synchronous and control broods, as there could be increased competition within a brood for the less available "Expensive Babyfood". In this case *c* chicks from control broods would be expected to achieve lower growth rates than synchronous *c* chicks. The results of this experiment suggest that switching from "Expensive Babyfood" to other prey is not controlled by the age of the *a* and *b* chicks, but no conclusion can be reached about the timing in relation to *c* chick age and whether the timing of the switch places *c* chicks at a disadvantage.

Effect of delayed incubation on hatching success

The effect of delayed incubation on hatching success has not previously been studied in the Herring Gull. However, in an investigation of hatching success of eggs of the Glaucous-winged gull *Larus glaucoides*, Reid (1987) found that delayed incubation of up to 8 days, had no effect. Comparing the results of his study and the results presented here, there is no difference between the two in the hatching success of the eggs where incubation was delayed (X^2 with Yates' correction = 0.14, 1 d.f., $P>0.1$). However, the hatching success of his control group was very low. If one compares the results for his experimental eggs against the hatching success of the control eggs on Walney, than the difference is highly significant (X^2 with Yates' correction = 18.44, 1 d.f., $P<0.01$). Reid's control group was too small (n=21) to make any meaningful comparison between the two (for there to be a significant difference in hatching success between eggs where incubation was delayed by 0 and by 2 days, those delayed by 2 days would have had to have a hatching success of less than 68%). He did find that the eggs where incubation was not delayed had the highest hatching success of any of his groups, the others ranging from 92% to 84%.

The difference between the results of the 2 studies appears to be due to the lower hatching success of his control eggs and the small sample sizes used by Reid. The hatching success of the control eggs in my study was exceptionally high (see table 6.8 for a comparison with other British studies). One possible explanation of this could be that the lower hatching success of the *a* eggs resulted in an increased hatching success of the *b* and *c* eggs. Herring gulls have been shown to neglect *c* eggs that are close to hatching, or even pipping, if the *a* and *b* eggs have hatched (Drent 1967, *pers obs.*). This has also been found to be true of Black-headed Gulls *L. ridibundus* (Beer 1966).

There remains the possibility that the low hatching success found in the eggs where incubation was delayed could be due to the conditions in which the eggs were kept. I think that this unlikley, as the eggs were well ventilated and kept at ambient temperature within

the colony and protected against direct insolation, the 3 main threats to hatching success in this manipulation (Drent 1975).

Comparing the hatching successes of delayed incubation *a* eggs with eggs from other British studies (Table 7.8), it appears that delayed incubation does have genuine adverse effect, as only two other British studies have recorded such low hatching success (the only studies where hatching success has been below 60% were Axell cited in Davis 1975, and Brown 1967). In both of these studies by far the highest cause of failure to hatch was predation. I therefore conclude that partial incubation of the *a* egg results is necessary in the Herring Gull, to ensure high hatching success.

Effects of supplementary feeding on chick growth and survival

The provisioning of supplementary food on territories during the first week after the *a* chick hatched resulted in higher fledging success per brood than that observed for control broods. This was a result of increased survival of both *a* and *b* chicks. No difference in survival was found between *c* chicks, however supplementary fed *c* chicks grew quicker and gained weight at a faster rate than did control chicks. This increased growth rate presumably puts the supplementary fed *c* chicks at an advantage, as growth rate normally has a positive influence on survival probability in gull chicks (e.g. Hunt and Hunt 1976).

In a similar experiment on the Isle of May, the provisioning of supplementary food during the first five days after the *a* chick hatched resulted in increased fledging success per brood and increased weight gains by chicks (although this increased weight gain was not a result of increased weight gain by any particular chick in the hatching order). The increased fledging success per brood was a result of increased survival of *c* chicks (Graves *et al.* 1984). These results agree with my findings that supplementary food increased fledging success per brood; however the pattern of increased survival and weight gain differ. A potentially important difference between the two studies is that the Isle of May study was carried out after many years of culling of adult Herring gulls. Presumably, at

least partly as a result of this and decreased competition, breeding success was exceptionally high during the year of study (control nests fledging an average of 1.26 chicks). This high "background" fledging success could explain the differences in mortality pattern between studies. Fledging success is normally higher for *a* and *b* chicks than for *c* chicks (Parsons 1972). If fledging success for control *a* and *b* chicks was high on the Isle of May, then the provisioning of extra food would not increase the fledging success of these, as these would normally receive sufficient food to survive. Instead, the survival probability of the less competitive *c* chicks would be increased (the chicks that would normally not survive). On Walney where the "background" survival of *a* and *b* chicks was lower, the extra food could result in increased survival. The extra food would perhaps not be sufficient in this situation to increase the survival of the *c* chick, as most of the "extra" would go to the competitively superior older chicks. The growth rate results support this interpretation, as while the supplementary fed *c* chicks gained weight and grew quicker than control *c* chicks, they did not gain weight at the same rate as their siblings.

Effect of supplementary feeding on adult attendance

Supplementary feeding resulted in increased adult attendance on territory, with an increased proportion of observations of two adults on territory, and a decreased proportion of observations of no adults on territory during the first week post-hatch. Graves *et al.* (1984) found a similar result for attendance by two adults during the first five days post-hatch. However in his study the level of attendance by two adults was much higher (control group between 40-50%, fed group between 50-70% compared with 11% and 19% respectively in my study).

The increased fledging success of supplementary fed broods could be a result of two factors; Firstly, increased adult attendance could result in better protection for young against predators, or result in increased brooding by parents. Secondly, as a direct result of increased food at a time when chick survival is food limited. Graves *et al.* (1984)

suggested that the former was not true, as the number of chicks dying per nest during the first five days post-hatch did not correlate with the percentage of time that both adults were on territory. Hunt (1972) found that exposure to predators resulting from parental absence during foraging was more important in chick survival than was the more infrequent feedings resulting from longer foraging distances. In the study by Graves *et al.* (1984), at least one adult was always on territory, so while protection of chicks may be increased with increased food availability, this cannot explain his findings. In my study however, during the first week post-hatch both adults were often absent from the territory (5% and 14% of observations for the supplementary fed and control groups respectively), so this could be a potential cause of the increased fledging success of supplementary fed broods. This seems unlikely however, as one would perhaps expect conspecific predation (the main source of predation in Herring gulls) to be random with regards to hatch order. This would not result in the differences in chick survival between groups being due to increased survival of the *a* and *b* chicks and not the *c* chick.

That it was the supplementary food that resulted in increased attendance, and not simply a random choice of poorer quality control nests, was demonstrated by the finding that adult attendance after the period of supplementary feeding was not different between the two groups. As the chicks grew, a difference between the two groups was found in the observations, with the control group having a higher proportion of observations where two adults were on territory. Rather than reflecting a meaningful difference, I assume that this finding was the result of increased foraging effort by the experimental group due to the larger brood sizes in this group. To control for this it would be necessary to compare adult attendance between the groups for each brood size, however this was not possible due to the small number of control nests with > 1 chick, and the small number of experimental nests with < 1 chick.

Effect of brood age on adult attendance

Several authors have argued that the high mortality observed in gull chicks during the first

week post-hatch cannot be due to any food limitation, as the energy demands of chicks at this time is at its lowest (e.g. Harris 1964). If this was true, then one would expect adult attendance to be highest during the first week post-hatch and for absence of adults to be at its lowest. Chicks are also at their most vulnerable to predation at this time, and their ability to thermoregulate is at its least developed so adults would be expected to brood more and protect chicks more at this stage. The E.B.H. however predicts that adults should be spending more time foraging at this stage, and therefore predicts that adult attendance should be comparatively low.

My observations clearly show that in spite of the low energy requirements of chicks at this stage and the chicks' need for protection and brooding, adult attendance at this stage is at its lowest. This is reflected in both the proportion of observations where no adults were in attendance, and the proportion of observations where two adults were present on territory. This strongly supports the E.B.H. and refutes the argument that foraging effort by the adults should be low at this stage.

In his study on the Holy Isle, Graves *et al.* (1984) found that the percentage of records where no adult was in attendance on territory increased with brood age and brood size, suggesting that adults were spending more time foraging as the brood became older. This is the exact opposite to my results. Unfortunately the exact methods of observation are not presented in Graves *et al.* (1984) so it is difficult to identify a possible methodological reason for this difference in findings. It is possible that parental absence on Holy Isle could have been due to persistent begging of chicks driving adults from the immediate vicinity of the brood. At Walney, adults were obviously driven away by persistent begging, however with the very high breeding density there, this resulted in the adults still being relatively close to the brood. On Holy Isle, the nesting density is much lower, with the gulls nesting mostly in a boulder beach strip around the island. Here it would be possible for adults forced away from the brood, to sit within sight of the brood, without actually being on territory. On Walney this was not possible as the area around the study site was

occupied by breeding gulls for several hundred metres in each direction. This could explain the difference between the findings of the two studies.

This interpretation of the observational results assumes that high adult attendance reflects a low foraging effort. This would seem to be a reasonable interpretation as it is difficult to envisage any activity other than foraging that could be more important than guarding/brooding the chicks, particularly during the first week post-hatch.

Synthesis

The results of this experimental investigation strongly support the E.B.H., and refute the current theories of hatching asynchrony in the Herring gull. My results demonstrate that hatching synchrony is advantageous and thus the premise of all other theories regarding hatching asynchrony i.e. that hatching is manipulated by adults to be asynchronous, so as to maximise breeding success, do not explain the pattern of reproduction observed in Herring gulls. A possible constraint on adults achieving hatching synchrony is identified in the experiment where partial incubation of the *a* egg was prevented. This experiment showed that partial incubation of the *a* egg, a cause of part of the hatching asynchrony observed in Herring gulls (Parsons 1972), is adaptive, as it is required to ensure that the *a* egg remains viable.

Herring gulls appear to attempt to maximise hatching synchrony by delaying full incubation of the *a* egg, so that the hatching span between the *a* and *b* egg is reduced. The reduction in size of the *c* egg reduces the hatching span between the *b* and the *c* egg. This explanation for the adaptive significance of the small size of the *c* egg is consistent with the E.B.H., while the conventional argument that it facilitates brood reduction does not predict the small size, as the degree of hatching asynchrony is more than sufficient to allow brood reduction to occur (see discussion of brood reduction hypothesis in chapter 7).

Whilst these experiments support the hypothesis that hatching synchrony is advantageous, this does not necessarily mean that the cause for this advantage is related to prey as the E.B.H. predicts. The results of the supplementary feeding experiment and the observational work however, match all of the predictions made by the E.B.H. and tell us more about the way that gulls organise their reproductive output in accordance with this hypothesis.

The supplementary feeding experiment shows that food availability during the first week post-hatch is a major factor controlling fledging success several weeks later. The

observations show that supplementary fed gulls appear to be able to decrease their foraging effort. The observations on broods of different ages demonstrate that in spite of the low energy requirements of chicks during the first week post-hatch, this is the time of highest foraging effort by the adults. This supports the idea that the "Expensive Babyfood" fed to the chicks during the first week post-hatch, is in fact more difficult for adults to provision their chicks with than prey that the chicks are capable of processing as they become older.

CHAPTER 9

GENERAL DISCUSSON

Population changes in Herring Gull at Walney

The results of the study of breeding success in 1990 suggest that breeding failure is not the cause of the dramatic decline in the number of Herring gulls nesting at Walney. The finding that egg volumes were very large, and that a very high proportion of breeding birds were in third year plumage suggest that competition amongst breeding birds for both food and nest-sites is extremely low.

Examinations of both adult diet and chick diet suggest that the availability of food for individual gulls has decreased since previous studies at Walney, which were carried out during the years of population expansion. As the number of breeding pairs has decreased, this suggests that the population level may be determined by food availability. This could offer an explanation for why the observed egg volumes were very large. Presumably competitively inferior birds would be more likely to desert Walney as their breeding success would be lowest (Drost *et al.* 1961). This would result in the mean quality of adults increasing with the possible result that mean egg volume would also increase. The finding that a high proportion of birds were breeding in third-year plumage suggests that this is not however the case. Young birds are competitively inferior to adults (Greig *et al* 1983).

During the period of population growth at Walney, the numbers of Herring gulls and Lesser black-backed gulls were equal (Vermeer 1977). However since then Herring gulls have suffered the major decline with Lesser black-backs having declined far less. In 1988, there were 8,000 pairs of Herring gulls and 17,000 pairs of Lesser black-backs (Dean 1991). Vermeer (1977) studied differences in the diet of these two species at Walney, and found that their diets were very similar, the only difference between the species being the areas in which they foraged. Lesser black-backs foraged more behind trawlers in the Irish Sea, on farmland further away from Walney than did Herring gulls, and relied less on the fish docks at Fleetwood, the refuse tip at Walney and the inter-tidal areas of Morecambe Bay.

The most important component of the diet of Herring gulls at Walney, is refuse. Sibly and McCleery (1986b) looked at the rate of energy intake of birds feeding on different food types around Walney, and from the rate of intake and the availability of different food types around Walney, concluded that Herring gulls could not breed on Walney if refuse was not available. Feeding on refuse may provide a high rate of energy intake, however it also carries a great risk to Herring gulls in the form of poisoning from *Clostridium botulinum* resulting in botulism (Lloyd *et. al.* 1991). During the decline in Herring gull numbers around Britain, mass outbreaks of botulism have occurred on many occasions at many different sites. In the summer of 1975 nearly 6000 birds, mostly Herring gulls, died in a series of outbreaks in Britain and Northern Ireland (Lloyd *et al.* 1976). Outbreaks have subsequently been reported from North East Scotland (Bell 1985), the Firth of Forth (MacDonald and Standring 1978), Orfordness (Shackles cited in Lloyd *et al.* 1991), south Wales (Sutcliffe 1986), many parts of Ireland (Buckley and O'Halloran 1986) and Guernsey (Hill cited in Lloyd *et al.* 1991).

The difference between the population dynamics of Herring gulls at Walney, and those of Lesser Black-backed gulls at Walney and Herring gulls at Sanda, could be due to their much heavier reliance on refuse resulting in death through botulism. The high resultant mortality would also explain why competition for nest sites and food prior to egg-laying have decreased (increased food availability resulting in increased egg volumes). This in effect, simulates the conditions produced by mass culling, and could produce the close similarity in results found between this study and those of Coulson *et al.* (1982) and Duncan (1978).

Another notable difference between the ecology of Herring gulls and Lesser Black-backed gulls, is that the former is resident in Britain, while the Lesser Black-back is a summer visitor that spends the winter months around the Mediterranean and North Africa (Cramp and Simmons 1983). It is possible that the difference in population dynamics between the

two species could be the result of changes in the winter quarters rather than the breeding grounds. This would not however explain why Herring gulls at Sanda have increased.

Causes for differences in population dynamics between colonies

The higher recorded breeding success at Walney than at Sanda would suggest that immigration should be occurring at Walney more than at Sanda. This depends on the populations mixing freely, which would seem likely as birds disperse away from the breeding colonies in winter. This is particularly true of first year birds from the Clyde area, a large number of which winter in North-West England and presumably mix with birds from Walney (Monaghan and Zonfrillo 1986). Maguire (1981) reported a chick ringed on Sanda being recovered as a breeding bird at Walney, demonstrating that interchange between the populations does occur.

The recorded breeding success at Sanda may however be an underestimate, as the nests studied over-represented newly colonised areas where breeding success was comparatively low. The older areas of the colony are probably more representative of the bulk of the population nesting on Sanda and also Sheep Island and Glunimore where breeding was first established. The breeding success in the oldest part of the colony on Sanda was extremely high, with 1.4 chicks per pair surviving to 4 weeks post-hatch.

The finding that Herring gulls breeding in the Clyde Sea area disperse into areas where birds from declining colonies also winter would suggest that they would be as likely to die from botulism as birds from say, Walney. This however depends on the timing of botulism infection. The occurrence of *Clostridium botulinum* increases during the summer months, particularly in pools of water where anaerobic conditions are found as a result of rotting vegetation and high temperatures. If the timing of peak infection is during the breeding season, or during late summer prior to dispersal to winter quarters, then birds from Sanda would be far less prone to infection than those from colonies where the main prey during the breeding season was refuse. Herring gulls are at their lowest body weight, and

mortality highest, immediately after the breeding season (Coulson *et al.* 1983*b*). At this time they are in poorest condition, and this may result in birds being more susceptible to infection.

Differences in population dynamics between the colonies at Sanda and Walney could be the result of two factors; Firstly, a decline in food availability at Walney as a result of a decrease in the amount of refuse tipped and a reduction in accessibility due to refuse being covered with soil more quickly. At the same time availability at Sanda has increased for all three main prey types. Second, the reliance of refuse by gulls at Walney may have resulted in large scale botulism, explaining why there has been no similar decrease in either Lesser black-backed gulls at Walney or the less refuse-reliant Herring gulls at Sanda.

Effect of diet on organisation of reproductive investment

The "Expensive Babyfood Hypothesis" (E.B.H.) is the only hypothesis regarding reproductive organisation in the Herring gull that is consistent with what is known of Herring gull breeding biology. However, many features of Herring gull breeding ecology are common to many other gulls and terns. These other species allow us to view the E.B.H. in context to species which may be very different to the Herring gull in terms of diet, body size and the habitats in which they live. This in turn allows us to identify whether the E.B.H. is merely an explanation for Herring gulls because it's predictions coincide with what is known of the Herring gull's biology, or whether it explains reproductive organisation in a group of species where the only thing they have in common ecologically is the way in which they organise their reproductive output.

Almost all larids lay a modal clutch size of two or three, with a smaller last laid egg (Cramp and Simmons 1983). As discussed in chapter 7, only the E.B.H. can offer any form of explanation for this. However, this explanation requires that each of these species should show either a difference in diet between small and large chicks, or that food must

be processed by e.g. partial digestion, for small chicks. The prey for small chicks must also be "expensive" i.e. the delivery rate in terms of energy/nutrients per unit time should be lower than for food given to older chicks. Studies of diet have not been made for all of the species of larid, and for many species where chick diet has been studied, differences in diet with chick age has not been investigated. In studies where the relationship between chick age and diet has been studied, the problem of whether apparent age related changes are in fact due to changes in availability, has not been addressed. However, the number of studies, and the wide range of species in which age related diet changes have been observed, suggest that this may be the normal situation in Larids. Of the Larids breeding in Europe, age related differences in chick diet have been documented for; Lesser black-backed gull *Larus fuscus* (Schaffer 1971), Herring gull *L. argentatus* (Schaffer 1971, Pierotti and Annett 1986, this study), Great Black-headed gull *L. ichthyaetus* (Borodulina 1960, cited in Cramp and Simmons 1983), Black-headed gull *L. ridibundus* (Creutz 1963, cited in Cramp and Simmons 1983), Roseate tern *Sterna dougalii*, (Cramp and Simmons 1983) Common tern *S. hirundo* (Boecker 1967, Lemmetyinen 1973, bith cited in Cramp and Simmons 1983) and Little tern *S. albifrons* (Culemann 1928, cited in Cramp and Simmons 1983).

Of the gulls breeding in Europe, only Little gull (*L. minutus*) feeds primarily on very small prey that would appear to be also suitable for chicks of all ages - insects. This is the only species of gull that appears to have a clutch size that is not truncated at three eggs as in the Herring gull and other Larids. Little gulls show the following clutch size distribution; C2 20%, C3 50%, C4 8%, C5 2%. This species would appear to be not controlled by prey switching as the other species are, as the prey that the adults feed on, and that is fed to all sizes of chicks, is the same. It is the only exception to the clutch size constraint predicted by the E.B.H. for species where "expensive babyfood" is required, and therefore supports the E.B.H. by suggesting that this constraint is diet related and not a feature common to all larids for some other reason.

An important prediction of the E.B.H. is that delayed incubation should result in decreased egg viability. If this is not the case, then larids should be able to delay incubation until the last egg is laid, and thereby achieve full hatching synchrony. The reason why larid eggs should not be able to withstand periods of cold prior to full incubation is not clear as many other species have developed chill tolerance in their eggs. This is particularly true of the Procellariiformes (see Boersma 1982) and some of the Alcidae e.g. Xantu's murrelet (*Synthliboramphus hypoleucus*; Murray *et al.* 1980) and Ancient murrelet (*Synthliboramphus antiquus*; Gaston and Powell 1989). The Procellariiformes and the murrelets are both characterised by long incubation and fledging periods (Drent 1975). The length of the incubation period correlates strongly with the length of the fledging period, suggesting that chick growth rate may be determined by embryonic growth rate (Drent 1975, Ricklefs 1983). In species where long periods of egg neglect occur as a result of adults having to feed far away from the nest e.g. Procellariiformes, slow embryonic growth rates may result in chill tolerance as eggs may require less heat to remain viable. In larids where chick mortality is high, selection has produced comparatively fast growing chicks and embryos to minimise time in the nest. A cost of this higher growth rate could be that as a result, egg cannot be chill tolerant. The relationship between chick growth rate, embryonic growth rate and chill tolerance warrants further investigation.

The E.B.H. makes predictions that could be of significance to the study of larid biology for the purpose of conservation. For example, in a situation where a rare larid was found to breeding unsuccessfully in an area due to chicks starving. A study from elsewhere, or an earlier study from that colony would assess the important components of diet as being those found most frequently in the diet. Prey fed to chicks during the first week post-hatch would form a relatively small part of the chick diet overall. However, the E.B.H. would predict that the prey fed to chicks less than 1 week old could be the most important in determining chick survival. Further work should be carried out to establish whether enhanced chick survival as a result of supplementary feeding could result in costs to either

breeding birds in terms of survival, or individual chicks as a result of decreased post-fledging survival. If these were found to have little or no effect, then populations of endangered larids could be artificially enlarged by providing supplementary food during the first week post-hatch, to increase breeding output.

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